

An Investigation into the Habitat
Requirements, Invasiveness and
Potential Extent of male fern,
Dryopteris filix-mas (L.) Schott, in
Canterbury, New Zealand

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Table of Contents

| | |
|--|-----------|
| Table of Figures | v |
| List of Tables..... | xi |
| Abstract..... | xiii |
| Acknowledgements | xiv |
| 1 Chapter 1 Introduction and Literature Review | 1 |
| 1.1 Introduction | 1 |
| 1.2 Taxonomy and ecology of <i>Dryopteris filix-mas</i> | 2 |
| 1.2.1 Taxonomic relationships | 2 |
| 1.2.2 Life cycle..... | 3 |
| 1.2.3 Native distribution | 4 |
| 1.2.4 Native habitat..... | 5 |
| 1.2.5 Mycorrhizal associations | 8 |
| 1.2.6 New Zealand distribution and habitat..... | 8 |
| 1.3 Invasion ecology and <i>D. filix-mas</i> in Canterbury | 10 |
| 1.3.1 Invasion ecology and invasive species..... | 10 |
| 1.3.2 Darwins naturalisation hypothesis (the importance of relatives) | 11 |
| 1.3.3 Niche Overlap | 12 |
| 1.3.4 The Rule of Tens..... | 13 |
| 1.3.5 Propagule pressure and dispersal | 14 |
| 1.3.6 Disturbance | 14 |
| 1.4 Thesis goals and approach | 18 |
| 2 Chapter 2 Effects of light environment on growth of <i>D. filix-mas</i> | 19 |

| | | |
|----------|--|-----------|
| 2.1 | Introduction | 19 |
| 2.2 | Method | 20 |
| 2.2.1 | Design and establishment | 20 |
| 2.2.2 | Light levels | 22 |
| 2.2.3 | Wet Pot Weights..... | 23 |
| 2.2.4 | Plant Weights | 23 |
| 2.2.5 | Statistical analyses..... | 24 |
| 2.3 | Results | 25 |
| 2.3.1 | Losses and Damage | 25 |
| 2.3.2 | Photosynthetically Active Radiation in each treatment | 25 |
| 2.3.3 | Wet pot weight change | 25 |
| 2.3.4 | Start weights of rhizomes..... | 26 |
| 2.3.5 | rhizome and roots, fresh weight change | 28 |
| 2.3.6 | Whole plant dry weight | 30 |
| 2.4 | Discussion..... | 31 |
| 3 | Chapter 3 Male fern habitat preferences in North Canterbury | 35 |
| 3.1 | Introduction | 35 |
| 3.2 | Study Sites..... | 35 |
| 3.2.1 | Tiromoana Bush..... | 36 |
| 3.2.2 | North Canterbury Foothills and inland sites..... | 38 |
| 3.3 | Methods | 43 |
| 3.3.1 | Data collection..... | 43 |
| 3.3.2 | Data entry and calculations | 45 |
| 3.3.3 | Ordination and analysis | 46 |
| 3.4 | Results | 47 |
| 3.4.1 | Tiromoana Bush..... | 47 |

| | | |
|----------|---|------------|
| 3.4.2 | North Canterbury foothills and inland sites..... | 58 |
| 3.5 | Discussion..... | 71 |
| 4 | Chapter 4 National distribution, range of observed habitats and the potential extent within New Zealand using Land Environments New Zealand. | 76 |
| 4.1 | Introduction | 76 |
| 4.2 | Method..... | 76 |
| 4.3 | Results | 77 |
| 4.4 | Discussion..... | 84 |
| 5 | Chapter 5 Summary and Conclusions | 90 |
| 5.1 | Overview..... | 90 |
| 5.2 | Habitat requirements in North Canterbury | 90 |
| 5.3 | Invasiveness and potential extent..... | 91 |
| 5.4 | Implications | 92 |
| 5.5 | Recommendations | 93 |
| 6 | Appendices | 95 |
| 6.1 | Appendix One Male Fern gallery | 96 |
| 6.2 | Appendix Two Field Data Form..... | 112 |
| 6.3 | Appendix Three Land Environments New Zealand attribute table for Level IV environments containing <i>D. filix-mas</i> | 114 |
| 6.4 | Appendix Four Species list..... | 120 |
| 7 | References..... | 128 |

Table of Figures

| | |
|---|----|
| Figure 1.1 Northern Hemisphere distribution of <i>D. filix-mas</i> (reproduced with permission from the Swedish Museum of Natural History website: http://linnaeus.nrm.se/flora/orm/polypodia/dryop/dryofil.html) | 4 |
| Figure 1.2 Confirmed records of <i>D. filix-mas</i> at commencement of this study from Lincoln Herbarium (yellow), NZ Biodiversity Recording Network (green), National Vegetation Survey (blue), literature and personal observation (red). (Base map from Google Earth). | 8 |
| Figure 2.1 Layout of replicates in the study area. A: full exposure, B: single layer of shade cloth, C: double layer of shade cloth, D: triple layer of shade cloth. | 21 |
| Figure 2.2 experiment layout and pot arrangement. View from replicate 8 (near left) to replicate 25 (centre distance) | 21 |
| Figure 2.3 Replicate groups used to obtain light level measurements | 22 |
| Figure 2.4 Wetpot mean percentage increase with CI ± 1 s.e. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth. | 26 |
| Figure 2.5 Regression lines for start weights~percentage increase, by treatment, with (top) and without replicate 29 (Treatment A: no shade), which was shaded by an adjacent structure during summer afternoons. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth..... | 27 |
| Figure 2.6 bar graph of mean rhizome start weight by treatment with replicate 29 removed. CI is ± 1 s.e. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth. | 28 |
| Figure 2.7 Regression for percentage increase in rhizome fresh weight. Slope = -0.0839 from Ancova with rhizome start weight as an additive covariable. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth. | 29 |
| Figure 2.8 Mean % increase/treatment (A n=7,B:D n=8) with ± 1 s.e. for “ treatment + start weight” as explanatory variables. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth..... | 30 |
| Figure 2.9 Mean total dry weight by treatment (A n=7,B:D n=8) with ± 1 s.e. for “ treatment + start weight” as explanatory variables. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth..... | 31 |
| Figure 2.10 Effects of treatments on frond form: Each column is 1 replicate, left to right Treatment D, 4% PAR, small thin fronds; Treatment C, 11% PAR, large thin | |

| | |
|---|----|
| fronds; Treatment B, 31% PAR, large, coriaceous fronds; Treatment A, no shade (100% PAR), small coriaceous fronds. | 34 |
| Figure 3.1 Map of North Canterbury with study sites indicated..... | 36 |
| Figure 3.2 An oblique view of the Tiromoana Bush study area viewed from the south with GPS plot points marked. Kate Valley drains through the bluffed gorge to the right (Image from Google Earth, 11 June 2010)..... | 38 |
| Figure 3.3 Mt Thomas plots from the east, pale forest is Douglas fir | 40 |
| Figure 3.4 Melrose plots from the southeast..... | 42 |
| Figure 3.5 Island Hills plots, the cluster at bottom left go from beech forest through kanuka to frost-hollow grey scrub. Remaining groups are in Douglas fir. | 43 |
| Figure 3.6 Tiromoana Bush DCA ordination plot and environmental factor relationships derived from species data for all tiers. Figure generated in Canoco Draw, note that Canoco limits names to 8 characters. Aspectx is aspect converted to degrees from North, therefore both East and West are 90°. Densi Mn (densiometer mean) is a proxy for light being a measure of how open the canopy is. Cpy cove (canopy cover) in this instance is a measure of gaps between canopy trees. | 48 |
| Figure 3.7 Species relationships from Axes 1 and 2 of the DCA for all tiers at Tiromoana Bush. <i>D. filix-mas</i> Δ is in the bottom left quarter. Dryland plants and high light are on the right..... | 49 |
| Figure 3.8 Samples and environment plot for Tiromoana Bush groundcover tier. | 51 |
| Figure 3.9 Tiromoana Bush DCA plot for groundcover species with rare species(less than 4 records) not shown for clarity. Group 1: cool with overhead shade but plentiful peripheral light from the forest edge. Group 2: high light, hot and dry. <i>D. filix-mas</i> , marked with \otimes | 52 |
| Figure 3.10 Distribution of plots with <i>D. filix-mas</i> at Tiromoana Bush within the ordinated space defined by axes 1 and 2 of the groundcover DCA. F-value 10.42, $P < 0.0018$ | 53 |
| Figure 3.11 Slope has no influence on <i>D. filix-mas</i> but most <i>D. filix-mas</i> are found on aspects to the South of East and West (>90 on y axis), $P=0.0067$ | 55 |
| Figure 3.12 Number of plots in each categorical environment category with the total number of plots with male fern at right (presence)..... | 56 |
| Figure 3.13 <i>D. filix-mas</i> occurrence expressed as the percentage of plots in each category that contain <i>D. filix-mas</i> | 56 |

| | |
|---|----|
| Figure 3.14 Mean number of <i>D. filix-mas</i> in plots of different surface shapes, standard error bars are 95% CI, $P < 0.0001$. Irregular surfaces are the uneven surfaces resulting from tunnel-gully erosion, slumping and landslides..... | 57 |
| Figure 3.15 Mean number of <i>D. filix-mas</i> in plots of different aspect, standard error bars are 95% CI, $P = 0.0002$ | 57 |
| Figure 3.16 Mean occurrence of <i>D. filix-mas</i> on different landforms, standard error bars are 95% CI, $P = 0.0435$ | 58 |
| Figure 3.17 Sample and environment plot for the DCA ordination of all tiers with the foothills and inland sites datasets. A possible arch effect on axis 2 is evident..... | 59 |
| Figure 3.18 Species plot for the DCA ordination of all tiers, with foothills and inland sites dataset. <i>D. filix-mas</i> is marked ⊗ | 60 |
| Figure 3.19 Sample and environment gradient plot from groundcover DCA with the foothills and inland dataset | 62 |
| Figure 3.20 Groundcover species DCA ordination for North Canterbury foothills and inland sites. Species with only one occurrence are not shown for simplicity. <i>D. filix-mas</i> is marked ⊗. In the upper left, species are characteristic of open sites and grey scrub, higher altitude and unmodified forest in the upper right, with <i>D. filix-mas</i> in the lower middle associated mostly with exotic species indicative of disturbance. | 63 |
| Figure 3.21 Axes 1 and 2 from the foothills and inland site groundcover ordination showing the distribution of plots with and without <i>D. filix-mas</i> | 64 |
| Figure 3.22 Axes 3 and 4 from the foothills and inland site groundcover ordination showing the distribution of plots with and without <i>D. filix-mas</i> | 64 |
| Figure 3.23 Plots with and without <i>D. filix-mas</i> against species richness. On the left for all foothills and inland plots ($P = 0.0069$) and on the right for non – plantation sites ($P = 0.001$)..... | 66 |
| Figure 3.24 Species diversity compared to light permeability with the non-plantation data. This plot is primarily to better illustrate the relationship of <i>D. filix-mas</i> to light permeability(Figure 3.25) and species diversity (Figure 3.23). <i>D. filix-mas</i> is rare with light permeability $< 7\%$ and conditions that favour species diversity also favour <i>D. filix-mas</i> (most <i>D. filix-mas</i> are in sites with more than 20 species). | 67 |
| Figure 3.25 Non-plantation, canopy light permeability for <i>D. filix-mas</i> presence, $P = 0.0275$ with mean and standard error of: absent - 18.8 and 1.1, and present 24.9 and 3.2. | 67 |

| | |
|---|----|
| Figure 3.26 Mean aspect: degrees from north for plantation plots with and without <i>D. filix-mas</i> (left) and a scatterplot that shows how these plots are distributed by aspect. The majority of plots with <i>D. filix-mas</i> are between 75° and 180° (ENE/WNW – S)..... | 68 |
| Figure 3.27 The relationship of foothills and inland plots with <i>D. filix-mas</i> relative to altitude (m). | 68 |
| Figure 3.28 The relationship of <i>D. filix-mas</i> to altitude in the non-plantation plots..... | 69 |
| Figure 3.29 The mean number of <i>D. filix-mas</i> by land shape and after backtransformation from GLM of family: quasipoisson, resulting in the rather extreme error bars. The graph on the left represents all foothills and inland plots; with plantation plots on the right. | 69 |
| Figure 3.30 Percentage of plots in each category that contain <i>D. filix-mas</i> from all foothills and inland sites..... | 70 |
| Figure 3.31 Distribution of plots with <i>D. filix-mas</i> from the foothills and inland site groundcover ordination. The drawn boundary provides a rudimentary indicator of plots which are likely to be suitable for <i>D. filix-mas</i> establishment based on their floristic similarity..... | 73 |
| Figure 4.1 357 records of <i>D. filix-mas</i> from New Zealand, many are overlain by adjacent points at this scale. Unverified records are those for which there is no reference to a voucher or photograph with which to verify the record, although the identification is from a reliable source e.g. Colin Meurk and Peter de Lange..... | 78 |
| Figure 4.2 Close-up from Figure 4.3 showing that records are not on the very low P sites. This area covers from Roturua in the top left to Murupara in the bottom right...81 | 81 |
| Figure 4.3 Acid soluble phosphorous from the LENZ underlying data. The scale ranges from < 7 mg/100 g (1 – 0) to 100 – 60 mg/100 g (5 – 4). Note the two records on the Chatham Islands (not included in LENZ) | 82 |
| Figure 4.4 Land Environments recorded as containing <i>D. filix-mas</i> (green) demonstrating the wide potential for this fern in New Zealand. | 86 |
| Figure 6.1 Typical shaded frond of <i>D. filix-mas</i> | 97 |
| Figure 6.2 A fully exposed fern from the experiment showing the dense golden scales typical of <i>D. filix-mas</i> , and the coriaceous pinnae as a response to exposure. | 97 |
| Figure 6.3 Underside of fertile <i>D. filix-mas</i> frond showing the kidney shaped indusia diagnostic of <i>Dryopteris</i> . In <i>D. affinis</i> the undusia edges roll right under..... | 98 |
| Figure 6.4 <i>D. filix-mas</i> is a popular garden plant in Canterbury, in this case Rangiora..... | 98 |

| | |
|---|-----|
| Figure 6.5 Wild <i>D. filix-mas</i> in a native grass bed outside the School of Forestry at University of Canterbury..... | 99 |
| Figure 6.6 <i>D. filix-mas</i> and <i>Dicksonia fibrosa</i> in the Ilam Gardens Christchurch..... | 99 |
| Figure 6.7 <i>D. filix-mas</i> growing from under a piece of limestone masonry on concrete at University of Canterbury..... | 100 |
| Figure 6.8 Epiphytic on a phoenix palm at Constance Bay, Timaru. | 100 |
| Figure 6.9 A rare occurrence on a north facing bank, but here shaded through summer by the cantilevered footpath (photo taken in winter), Timaru. | 101 |
| Figure 6.10 Rather robust <i>D. filix-mas</i> at Hanging Rock, South Canterbury. (Photo A. Shanks)..... | 101 |
| Figure 6.11 Regrowth on a road bank after mowing. Unusual in that the substrate is Separation Point granite (low fertility and low pH), Orinoco Valley Rd, Ngatimoti, Tasman..... | 102 |
| Figure 6.12 Tall <i>D. filix-mas</i> on a road bank near the Conway River, which has had the brushweeds (broom and blackberry sprayed out). | 102 |
| Figure 6.13 Above the Rakaia River with broom and <i>Cotoneaster simonsii</i> | 103 |
| Figure 6.14 Heavy growth of <i>D. filix-mas</i> at the edge of Douglas fir plantation, with a few <i>Polystichum vestitum</i> mixed in. Island Hill, Island Hills Station..... | 103 |
| Figure 6.15 One <i>D. filix-mas</i> (left) and one <i>P. vestitum</i> in a light gap in Douglas fir. Island Hills Station..... | 104 |
| Figure 6.16 Under sycamore (<i>Acer pseudoplatanus</i>) in the Mandamus Valley, North Canterbury..... | 104 |
| Figure 6.17 A rare occurrence, <i>D. filix-mas</i> under beech forest (<i>Fuscospora solandri</i>), with <i>P. vestitum</i> (left). In this case a heavily grazed remnant on Melrose Station, North Canterbury..... | 105 |
| Figure 6.18 To the left of this fertile <i>D. filix-mas</i> at Tiromoana Bush there are at least seven sterile <i>D. filix-mas</i> sporophytes. | 105 |
| Figure 6.19 Under the edge of a <i>Cupressus</i> plantation, <i>D. filix-mas</i> has established with <i>Blechnum penna-marina</i> , <i>B. fluviatile</i> and <i>P. vestitum</i> . Loburn, North Canterbury..... | 106 |
| Figure 6.20 <i>D. filix-mas</i> (browsed on right) with <i>D. dilatata</i> , <i>B. penna-marina</i> and <i>P. vestitum</i> in a gap between <i>Pinus radiata</i> and Douglas fir at Island Hills Station..... | 106 |

| | |
|---|-----|
| Figure 6.21 <i>Dryopteris xtavellii</i> , the hybrid between <i>D. filix-mas</i> and <i>D. affinis</i> , with small plants of <i>D. filix-mas</i> on either side. Rakaia. | 107 |
| Figure 6.22 <i>D. filix-mas</i> in the side of a rock ravine on Melrose Station in North Canterbury. The site itself is not grazed but the slopes above are and the ravine itself probably has a history of fire and aerial fertiliser application. | 107 |
| Figure 6.23 Under grey scrub (<i>Discaria toumatou</i> and <i>Coprosma propinqua</i>) In the Lewis Pass. | 108 |
| Figure 6.24 Emerging from under rubble at the base of an alluvial terrace in the Lewis Pass. | 108 |
| Figure 6.25 <i>D. filix-mas</i> on limestone talus in Mead Stream, Clarence Valley. | 109 |
| Figure 6.26 The semi-arid Tweed basin below Lake McRae in Molesworth Station. <i>D. filix-mas</i> can be found in the incised gullies (bottom right) and along the stream under the crack willow (<i>Salix fragilis</i>). | 109 |
| Figure 6.27 At Hell's Gate in the Wairau Valley, Marlborough, <i>D. filix-mas</i> grows amongst the rocks and scrub on the avalanche path that occupies the middle of the photo. At the time of the photo (2014) <i>D. filix-mas</i> were not present within the beech forest. | 110 |
| Figure 6.28 <i>D. filix-mas</i> in an avalanche path at Hell's Gate, Marlborough. | 110 |
| Figure 6.29 <i>D. filix-mas</i> emerging from deep within a rock pile at Hell's Gate, Marlborough. | 111 |
| Figure 6.30 <i>D. filix-mas</i> growing by the Wairau River, amongst speargrass (<i>Aciphylla aurea</i>) and grey scrub at Hell's Gate. | 111 |

List of Tables

| | |
|---|----|
| Table 2.1 Photosynthetically active radiation (PAR), transmitted by the different shade cloth treatments. Percentage of PAR averaged from four replicates/treatment, repeated on three days. | 25 |
| Table 2.2 Significance (P) values for change in wet pot weight from Tukey's Honest Significant Differences Test. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth. | 26 |
| Table 2.3 Comparison co-efficients for percentage change in fresh weight with start weight as a co-variable. Adjusted R-squared: 0.79; F-statistic: 28.47 on 4 and 26 DF; overall p-value: 3.657e-09 A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth. | 29 |
| Table 2.4 Tukey HSD test results for shade treatments with whole plant dry weight. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth..... | 30 |
| Table 3.1 Summary statistics for the Tiromoana Bush DCA ordination axes | 50 |
| Table 3.2 Summary of one way Anova output for <i>D. filix-mas</i> presence against DCA ordination axes. (Degrees of freedom = 1 with 76 residuals in each instance). | 54 |
| Table 3.3 Significance of environmental factors for <i>D. filix-mas</i> presence/absence from Anova..... | 54 |
| Table 3.4 Significance values for the categorical explanatory variables at Tiromoana Bush..... | 55 |
| Table 3.5 Summary statistics for foothills and inland sites DCA ordination axes | 61 |
| Table 3.6 Results from Anova for the axes of the foothills and inland sites groundcover DCA ordination. P is significant at: *** 0.001, ** 0.01, * 0.05..... | 62 |
| Table 3.7 Significance (P values) of the presence of <i>D. filix-mas</i> for the continuous variables in the foothills and inland sites dataset from GLM. Significance level codes: *** 0.001; ** 0.01; * 0.05..... | 65 |
| Table 3.8 Contrasts of the land shape levels using releval in R..... | 70 |
| Table 3.9 Summary of the occurrence of <i>D. filix-mas</i> with aspect, landform and landscape for foothills and inland plots and the subsets plantation and non-plantation | 71 |
| Table 4.1 Indicative proportion of New Zealand susceptible to colonisation by <i>D. filix-mas</i> as determined by known occurrence within LENZ environments at the four levels of Land Environments New Zealand | 79 |

| | |
|--|----|
| Table 4.2 and Table 4.3 summary elevation and climate data of the LENZ Level IV attributes as taken from the attributes table for the Level IV raster file. The minimum and maximum values for all 500 of the Level IV environments are presented first, followed by comparative data for the 105 environments in which <i>D. filix-mas</i> has been recorded..... | 80 |
| Table 4.4 Principal LENZ environments containing <i>D. filix-mas</i> | 83 |

Abstract

The vegetation of New Zealand has undergone extreme changes during the period of European settlement, with not only forest clearance but a deliberate attempt to replace the native vegetation with species from Europe and later from other parts of the world. Garden escapes continue this process to the current day.

Several European ferns that have been introduced to New Zealand gardens have subsequently escaped. At the time of writing *D. filix-mas* is the most obvious and probably the most abundant in the rural areas of Canterbury having been observed in a wide range of habitats from suburban to farm, to forests both plantation and montane and in shrublands.

This thesis investigates some of the ecology of *D. filix-mas* and explores its potential as a weed detrimental to New Zealand's indigenous ecosystems. An extensive literature review revealed that in the Northern Hemisphere *D. filix-mas* grows over a wide range of climates, vegetation types and soils. However the literature review did not clearly show the forest light conditions under which *D. filix-mas* grows nor could the Northern Hemisphere experience in deciduous woodlands and coniferous forests be directly carried over into New Zealand's podocarps, evergreen hardwood and evergreen beech forests. An experiment was designed to investigate tolerance to shade and field data was collected at several sites across North Canterbury for subsequent investigation with ordination and standard statistical methods. Records from around New Zealand were collated and used to generate a map of potential extent using the Land Environments New Zealand dataset.

Positive growth was achieved under all shade treatments including the heaviest at 96% shade. However the field data suggests that under some of the lowest light availability *D. filix-mas* does not grow. In the field *D. filix-mas* is found in diverse habitats with a preference for sheltered sites with more southerly than northerly aspects. Interpretation of the ordination output combined with knowledge of the sites suggests that *D. filix-mas* is mostly associated with degraded sites and sites of past disturbance. Regenerating kanuka is a reliable place in which to find *D. filix-mas* but relatively natural beech forest is not. *D. filix-mas* can potentially grow over much of the South Island particularly in drier areas and can be invasive following disturbance and when grazing is removed, making it a potential problem for indigenous forest restoration efforts.

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1 Chapter 1 Introduction and Literature Review

1.1 Introduction

Male fern, *Dryopteris filix-mas* (L.) Schott, is becoming a common exotic species in several parts of New Zealand. Where previously *D. filix-mas* was considered a weed of some urban and suburban areas (e.g. Christchurch and Dunedin) it is becoming a regular component of rural vegetation from unimproved hill country pasture, to exotic forest and indigenous forest remnants. For example the Queen Elizabeth II National Trust, Canterbury field officer, doubts that there are any forest/shrub covenants in North Canterbury where *D. filix-mas* is not present (M.Giller pers. comm. 2010). Personal encounters with *D. filix-mas* during forest inventory on North Canterbury farms from 2003 to 2009 include rough hill country pasture, among brush weeds, grey scrub, exotic forest and indigenous forest remnants. Leon Perrie, a botanist at the Museum of New Zealand –Te Papa Tongarewa, considers that *D. filix-mas* may be present in at least 50% of South Island forests he enters although seen less frequently on the West Coast (L.Perrie pers. comm., 2010). However the question of whether *D. filix-mas* is opportunistically occupying degraded sites or is detrimentally invasive is open to debate.

D. filix-mas was first recorded as an adventive plant in 1958 (Webb et al. 1988). Webb et al. (1988) describe *D. filix-mas* as “...an aggressive coloniser...spreading rapidly in...the South Island.” Despite this, it has only recently been acknowledged as an ecological weed being first listed by the Dept. of Conservation in 2008 (Howell 2008). On Banks Peninsula, botanist Hugh Wilson rates *D. filix-mas* as a moderately serious weed, recommending removal if possible (Dept of Conservation 2010). Also on Banks Peninsula, *D. filix-mas* is considered a threat to rocky outcrop vegetation (Parks 2008). On Otago Peninsula, *D. filix-mas* is considered to pose an ongoing threat to forest ecosystems (Johnson 2004). On Otamahua/Quail island in Lyttleton Harbour, *D. filix-mas* is considered a problem weed (Burrows and Watson 2000, Norton et al. 2005) and despite constant removal from Otamahua it continues to reappear (C. Burrows pers. comm. 2010).

Elsewhere it seems that *D. filix-mas* continues to be overlooked as a problem weed or else is considered a low priority. For example, *D. filix-mas* is identified as a weed in the

village of St Arnaud where a few small populations were removed some years ago, but control effort has lapsed (D. Chisnall pers. comm. 2010). Invasion of undisturbed indigenous vegetation may be slow, for example *D. filix-mas* was first recorded in the kanuka forest at the Eyrewell Scientific Reserve in 2001-2003 (Ecroyd and Brockerhoff 2005), although the arrival of *D. filix-mas* and *Hypolepis ambigua* may be due to "...a change to wetter, shadier and more sheltered understorey conditions,..." (Ecroyd and Brockerhoff 2005, p 286). Personal experience also does not suggest that *D. filix-mas* is an immediate threat to intact forest ecosystems, even though it has all the hallmarks of a successful invasive species in New Zealand. However Leon Perrie (pers. comm. 2010) considers that it is capable of invading "relatively intact forest" A paucity of records in the National Vegetation Survey database (NVS)(online search) would suggest that *D. filix-mas* remains rare in natural environments.

The habitat requirements of *D. filix-mas* seem to be poorly understood and there do not appear to have been any prior studies of the roles that *D. filix-mas* may have in indigenous New Zealand ecosystems. It may prove to be aggressive or benign in undisturbed habitats, it may assist or disrupt restoration of degraded sites, and it may displace or be displaced by indigenous ground ferns.

D. filix-mas is joined in NZ by 3 related deciduous European ferns, *D. dilatata*, *D. affinis* and *Athyrium filix-femina*, of these only *D. affinis* is locally common and is apparently restricted to in and near urban areas. The evergreen *Polystichum* are also very closely related, with one Australian and one European *Polystichum* occasionally escaping cultivation in New Zealand.

1.2 Taxonomy and ecology of *Dryopteris filix-mas*

1.2.1 Taxonomic relationships

Dryopteris is a large genus of mostly Northern Hemisphere ferns comprising c. 225 species (Hoshizaki and Wilson 1999) in the family Dryopteridaceae, some 50 – 80 genera occur in this family depending on treatment. 10 genera are found in New Zealand (Brownsey and Smith-Dodsworth 2000) *Athyrium*, *Cyrtomium* and *Dryopteris* are adventive, with adventive and indigenous species in *Cystopteris* and *Polystichum*. *Lastreopsis*, *Rumorba*, *Arachnioides*, *Diplazium* and *Deparia* have no introduced species in New Zealand although *Deparia petersenii* (Kunze) Kato, mistakenly treated as *Athyrium*

japonicum by (Allan 1961), was first recorded from New Zealand in 1906 (Brownsey and Smith-Dodsworth 1989); it is not included as an adventive species in the Naturalised Flora of New Zealand (Webb et al. 1988) presumably as New Zealand is a natural range expansion although anthropogenic disturbance may have facilitated the expansion. *Dryopteris* and *Polystichum* are very closely related with several Northern Hemisphere species having been placed in both genera, at different times. The principal distinguishing features in New Zealand are the round indusium of *Polystichum* compared to the kidney shaped indusium of *Dryopteris*; absence of hairs in *Dryopteris* (scales present) and where indigenous *Polystichum* fronds are persistent and coriaceous, the adventive *Dryopteris* tend to be deciduous and thin, making separation of the genera straight forward.

D. filix-mas is a tetraploid ($2n = 164$ compared to 82 for the genus) which is thought to have originated from a hybrid between *D. oreades* and *D. caucasica* (Fraser-Jenkins 1986). However with numerous additional hybrids there has been much confusion over the number of species and the relationships between various taxa. For example the apogamous triploid, *D. affinis* ssp. *borreri* (Hoshizaki and Wilson 1999) is referred to as *D. borreri* by Wagner (1951) who comments that it has often been included in *D. filix-mas*. A further example comes from a 1936 fern catalogue from Perry's, England, listing 33 varieties of *D. filix-mas*, 7 for *D. dilatata*, and 62 for *Athyrium filix-femina* (Benedict 1936) but Hoshizaki and Wilson (1999) comment that there is much confusion with the naming of cultivars (including *D. affinis*) and that this is perpetuated in garden centres. However *D. filix-mas* s.s., as an abundant and readily available fern through Europe, has been used for studies involving reproduction and development of gametophytes e.g. (Korpelainen 1994, 1995, 1996).

1.2.2 Life cycle

D. filix-mas is perennial and homosporous with numerous spores released in autumn, producing gametophytes which can be male, female, hermaphrodite or asexual (Korpelainen 1994). Female gametophytes are large, cordate and may develop into hermaphrodites, while males are small and spatulate (Barker and Willmot 1985). Sporophytes may be produced by intragametophytic selfing, intergametophytic selfing and intergametophytic crossing (Korpelainen 1996). With poor nutrition fewer gametophytes are hermaphrodite and these are less likely to produce a sporophyte

(Korpelainen 1994). Mature gametophytes produce antheridiogens preventing immature neighbouring gametophytes from developing archegonia. This may have two purposes, firstly to increase the cross-fertilisation opportunities for the gametophyte and secondly to reduce competition for the resultant sporophyte from intra and inter-specific sources (Korpelainen 1994).

Young sterile sporophytes may have several flushes of relatively short-lived fronds with the later fronds remaining green through winter (Bauer et al. 1991), while mature plants typically have a single flush of fronds in spring which die down in autumn. In Canterbury both sterile and fertile sporophytes may remain green through the winter (pers. obs.).

1.2.3 Native distribution

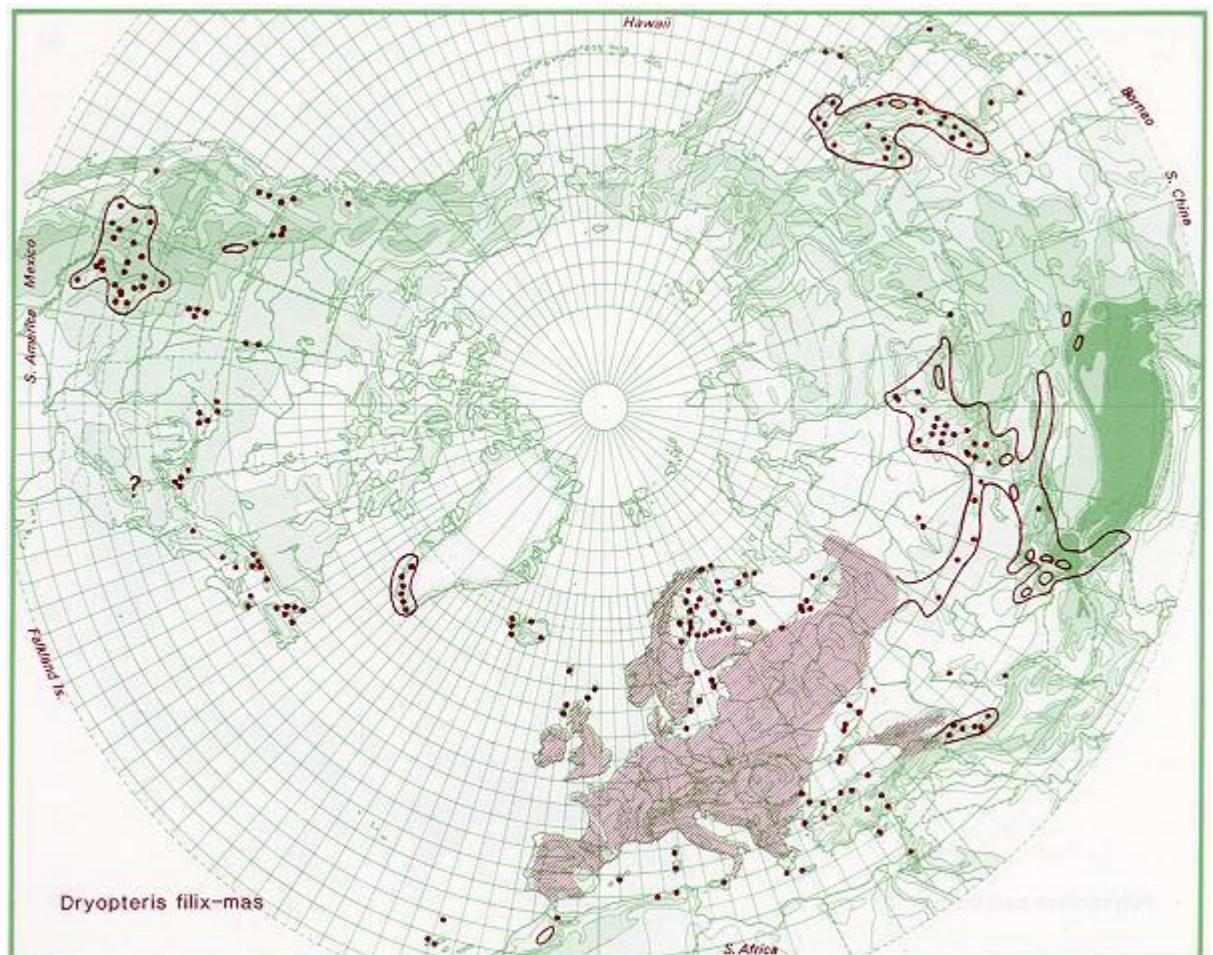


Figure 1.1 Northern Hemisphere distribution of *D. filix-mas* (reproduced with permission from the Swedish Museum of Natural History website:
<http://linnaeus.nrm.se/flora/orm/polypodia/dryop/dryofil.html>)

D. filix-mas is generally considered a species of temperate to hemiboreal forests in the Northern Hemisphere. It is considered to be the most abundant and widespread fern in Britain, being found throughout (Perring and Walters 1962). It is also widespread through Europe into the Himalaya, Asia and North America. In North America it occurs in 2 main areas: in the northwest it grows along the Rocky Mountains from British Columbia in Canada into Mexico (USDA 2010) with outliers in the Sierra Nevada and San Bernadino Mountains of California (UC/JEPS 2010). In the north east it occurs around the Great Lakes eastward to New Foundland and the southern tip of Greenland. Latitudinal range is not stated however the map above takes it to over 70°N (the Arctic Circle is c. 66 °N), while crossing into Mexico takes it down to at least 30°N and the Canary Islands to c. 28 °N.

1.2.4 Native habitat

D. filix-mas is primarily a species of moist and fertile forests particularly deciduous forest, but is also found in a wide range of other habitats including open ground and stone/brick walls in towns (Brandes 1995), open ground in natural settings (Burga 1999) and under deciduous scrub in dune hollows (Willis et al. 1959). In German railway stations *D. filix-mas* was found on track beds, between tracks, on platform walls and in mortar joints of other walls (Wittig 2002). In Finland, *D. filix-mas* grows on railway embankments traversing forest and semi-open sites (Suominen 1969). *D. filix-mas* first appears in glacial succession at Morteratsch in Switzerland (46°27' N; 9°56'E) on 27 year old surfaces against boulders and other moist sites on coarse substrates, (Burga 1999). The altitude here is 2 100m a.s.l. (Burga 1999) but Vittoz et al. (2008) give a maximum altitude in this area for *D. filix-mas* of 2540m. Further up this valley in the alpine belt (>2300m) is Isla Perla, an ice free spur, which has been studied since 1906. *D. filix-mas* arrived here between 1995 and 2004, where it occurs on fresh stones and gravel (Vittoz et al. 2008). In Poland, *D. filix-mas* is the most common *Dryopteris* ranging from lowland deciduous woods and tall herb communities up to 1770m a.s.l. in sub-alpine *Pinus mugo* and spruce forests (Ivanova and Piekos-Mirkowa 2003). In North America *D. filix-mas* occurs in dense woods in the north-east and open woods among boulders in the west with an altitude range of 200 – 2500m (eFloras 2010).

The Ellenberg Indicator values (Ellenberg 1979) are widely used in Europe to describe the environmental conditions in which different species are most commonly found,

although species with wide tolerances may be found well outside the parameters indicated by the Ellenberg value. These values are loose and only applicable to European plant communities, however they do serve to indicate where a species might be found or alternatively the conditions that might be expected where a given species is found. In *Zeigerwerte der Pflanzen Mitteleuropas* (Ellenberg and Leuschner 2010) with English definitions summarised from Hill et al. (1999), the values indicate: Light < 5%, seldom more than 30% when plants are in full leaf; Temperature – not indicative; Moisture – fresh soils of average dampness; pH – moderately acid to weakly alkaline; Fertility (N) – intermediate to rich soils. For Britain, Hill et al. (1999) gave: Light >10% when trees are in full leaf and rarely in full light; Moisture – between average dampness and always moist (not wet); pH – no change; Fertility (N) – intermediate.

While moderately acid, moist and fertile soils appear to be the optimum soil type, many studies encounter *D. filix-mas* on limestone talus and basaltic soils (Pigott and Taylor 1964, Cooper 1984, Parks 2008). In the Tatras Mountains (Poland) *D. filix-mas* is found on several soil types but is most common on limestone rendzinas (Ivanova and Piekos-Mirkowa 2003). Rendzinas are dark, humus rich soils formed on calcareous parent material with a pH between 6.4 and 8.1 (Dixon 1991). *D. filix-mas* is also found on granites and granitic rocks (Vittoz et al. 2008) which tend to produce acid soils. In North America, *D. filix-mas* occurs on granitic and igneous rocks in the west and on limestone talus in the north-west. In southern Sweden *D. filix-mas* occurs over a pH range of 4.0 – 6.5 (Falkengren-Grerup 1986), and is positively correlated to total soluble aluminium in soils (Falkengren-Grerup et al. 1995) which is higher in low pH soils (During 1984).

Climatic data is scarce, Hoshizaki and Wilson (1999) state that *D. filix-mas* is “...tolerant of somewhat drier sites than other *Dryopteris* species.” and hardy to a January average of 20°F (c.-7°C), but do not explain whether this is for the foliage or the rhizome. Vittoz et al. (2008) give mean temperatures of “...-7.2 ± 1.9°C in January and 10.4 ± 1.2°C in July...” 15km away and 700m lower than at the west facing Isla Perla study site. Using a fine weather adiabatic lapse rate of 10°C/1000m, would lower these temperatures by 7°C but takes no account of micro-climate effects such as snow insulation in winter and local heating effects at ground-level on a western aspect. However this still indicates a fair tolerance of winter freezing and limited growing seasons. There is no mention of

rainfall, which would in any case be misleading, as soil moisture availability over summer is more likely to be relevant. While climate data might be extrapolated from readily available national weather data such as rainfall and temperature maps, these may also be misleading as *D. filix-mas* is occurring at micro-sites in the larger landscape and the distribution data available does not provide enough detail for this purpose.

Shade and light tolerance may be inferred to cover a wide range. In a functioning coppice wood, Ash and Barkham (1976), found *D. filix-mas* in semi-mature coppice rather than freshly cut and mature (dense) stands, implying that coppice growth at maturity excludes sufficient light to eliminate *D. filix-mas*. Piggott and Taylor (1964) recorded *D. filix-mas* in light conditions from dense shade to almost fully exposed (no plots were fully exposed) on west facing limestone scree in Derbyshire, England. *D. filix-mas* has also been found to be phototropic to red light which is considered to be an adaptation to low light in ferns (Kawai et al. 2003).

Looking at community structure, slope, soil depth, moisture and disturbance Cooper (1984) studied composition of a deciduous wood on a basaltic talus slope in Northern Ireland. A reciprocal averaging ordination placed *D. filix-mas* in a position corresponding to moderate levels of disturbance and moderate soil moisture. However stand ordination identified 5 communities from wet stable sites low on the slope to well-drained mobile sites with little soil, *D. filix-mas* was found in all communities.

In summary, *D. filix-mas* grows in a wide range of vegetation types; over a wide range of latitude ($< 30^\circ$ to $> 70^\circ$); across a wide climatic range from mild, maritime sites to montane to continental interiors; on young and old soils commonly with a pH of 4.0 – 6.5 but also tolerating alkaline soils with a much higher pH; is tolerant of high levels of aluminium; tolerates a wide range of light/shade levels and would appear to be quite tolerant of freezing. From the literature it appears that *D. filix-mas* has a preference for moist forest soils, but also does well in harsh habitats characterised by scree, stones, boulders and their human equivalents provided by walls, railway ballast and waste ground, these latter sites are also characterised by regular disturbance. There is no suggestion that these represent two ends of a continuously occupied range, rather in its natural range competition from other species may prevent occupation of intermediate

habitats by *D. filix-mas*, or dry forest soils may simply be unsuitable for sporophyte development and survival.

1.2.5 Mycorrhizal associations

D. filix-mas readily forms, but does not require root associations with arbuscular mycorrhiza and ecto-mycorrhiza (Hepden 1960, Cooper 1977, Harley and Harley 1987). Mycorrhizal association produces growth benefits when available P is low ($4\mu\text{g}/\text{ml}$ of soil) (Cooper 1977) and may assist with drought hardiness although this is not mentioned in the literature for *D. filix-mas*.

1.2.6 New Zealand distribution and habitat

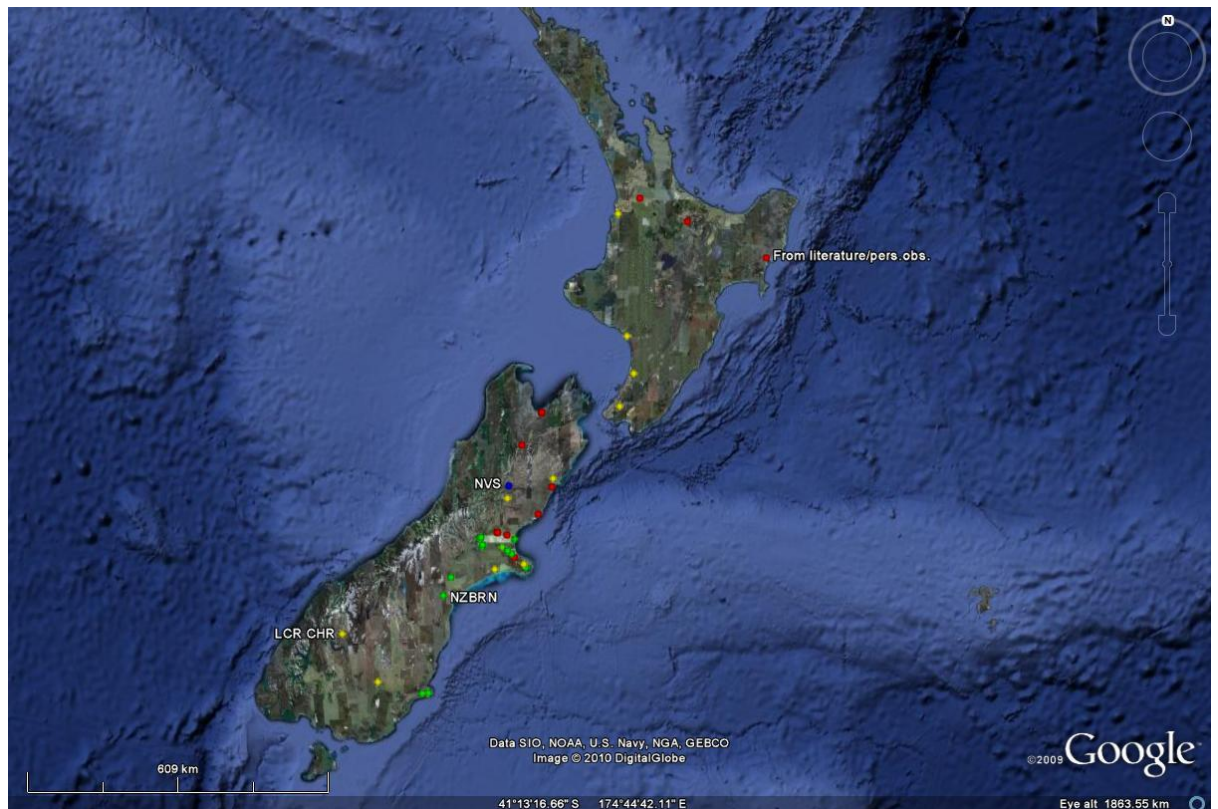


Figure 1.2 Confirmed records of *D. filix-mas* at commencement of this study from Lincoln Herbarium (yellow), NZ Biodiversity Recording Network (green), National Vegetation Survey (blue), literature and personal observation (red). (Base map from Google Earth).

D. filix-mas is widespread in New Zealand with herbarium material from Hamilton in the north to Dunedin in the south (Figure 1). Webb et al. (1988) also give a Southland record and describe the habitat as “Cemeteries, road and railway banks, drains, streamsides, open scrub, damp forest.” In Canterbury *D. filix-mas* may be found in fully

open sites where terrain provides shade (pers. obs.) mirroring the Finnish railway experience where *D. filix-mas* is more common on cooler north facing embankments (Suominen 1969). Known distribution and abundance of records are probably artefacts of anthropogenic dispersal and recording/collection effort. Records in Figure 1.2 are associated with large population centres (Hamilton, Rotorua, Gisborne, Wanganui, Wellington, Nelson, Christchurch and Dunedin) reflecting the opportunities for anthropogenic dispersal. The origin of New Zealand plants is not known but given that many existing populations and herbarium specimens are of decorative forms they have probably been introduced and further propagated for their aesthetic/novelty values and hardiness particularly in Canterbury where decorative native ferns require particular care in the dry climate. The scale of this planting can be illustrated by a North Canterbury farmer coining the name ‘Fendalton fern’ for *D. filix-mas* after the suburb in Christchurch where he went to school (D. Shand pers. com. 2009). Herbarium collections are unlikely to be representative particularly in the case of Canterbury where there is a relatively large number of resident botanists which may influence the frequency of records e.g. most of the New Zealand Biodiversity Recording Network (NZBRN) records (green points in fig. 1.2) are by one Landcare Research botanist.

North Canterbury plants are associated with silt loams (loess), scree and soils derived from calcareous mudstone (pers. obs.); Banks Peninsula plants would appear to be associated with loess, basaltic soils and basaltic rock outcrops (Parks 2008). Three records come from mountain areas: Mt Aurum Station near Queenstown; near treeline in the Mandamus River, west of Culverden and in the Waiau Gorge on Glenhope Station (NVS in Fig. 1). Other NVS records are near Christchurch and Dunedin. Prior to the September 2010 earthquake and devastating February 2011 earthquake, *D. filix-mas* could occasionally be seen growing from weathered/cracked brick and masonry in Christchurch (pers. obs.). In a Christchurch woodland study, *D. filix-mas* was most abundant in “exotic dominated garden woodland” (Stewart et al. 2009, p 157) reflecting the common occurrence of *D. filix-mas* in Christchurch gardens. Ordinations positioned *D. filix-mas* away from native dominated and semi-wild woodlands. While the range of habitats utilised by *D. filix-mas* was not presented, this study points to a preference for some disturbance and deciduous woodlands but does not preclude native habitats.

The only NZ information on climate is that fronds from a Dunedin provenance begin to experience freezing damage at -9°C (Bannister 1984). However a wide range of climatic tolerance can be inferred from the known distribution: mild, humid, maritime lowlands to summer dry, sub-continental, sub-alpine sites. Bannister and Wildish (1982) carried out the most relevant study in Dunedin, New Zealand. They studied *D. filix-mas* and three native ferns (*Asplenium bulbiferum*, *Polystichum vestitum* and *Phymatosorus pustulatus*) under different light conditions and found that all four species had adaptive responses to low light. They exhibited a phenotypic response to low light conditions with an increased specific leaf area which was correlated with a decrease in light compensation point. For *D. filix-mas* the light compensation point also decreased considerably with temperature.

1.3 Invasion ecology and *D. filix-mas* in Canterbury

D. filix-mas is well established in some parts of New Zealand and establishing in other parts. In Canterbury, *D. filix-mas* is widespread and increasing in abundance at a local scale while continuing to disperse at the landscape scale. Despite *D. filix-mas* having successfully established, the principles of invasion ecology continue to apply to establishment at new locations and in habitats of a type that it has not yet established in. Each such site can be considered a fresh invasion, consequently the principles of invasion ecology continue to be relevant to the speed with which *D. filix-mas* enters that site (if it does at all), the effect it has on the community at that site and the point at which it achieves equilibrium.

1.3.1 Invasion ecology and invasive species

Invasion is the process of a foreign species establishing itself in a new area or habitat in which it has not previously occurred. We tend to associate this with anthropogenic assistance (introduced organisms) although it may also be by changes in the environment or genetic shifts in a species allowing it to occupy a site where it was previously unable to survive. Plants that succeed in establishing a viable population in a new site are generally called adventive or naturalised when well established. Some authors use invasive for all adventive species .e.g. Williamson (1996), others distinguish between naturalised and invasive e.g. “...invasives...have a demonstrable ecological or economic impact.” (Lockwood et al. 2007, p 8). This definition of invasive has been adopted for this study.

Invasion ecology seeks to explain: how invasions occur; the likelihood that an imported species will become invasive; how fast an invasive species will spread; whether or not it will become problematic in various contexts. Developing predictions about invasions has however proven difficult, such that where a rule is established there are always examples that do not fit the rule (Williamson 1996). Rules for invasion ecology then are more generalisations, offering some guidance. Several theories and general rules relevant to *D. filix-mas* are discussed below and summarised in Table 1.

1.3.2 Darwins naturalisation hypothesis (the importance of relatives)

Darwin put forward a theory which is now called ‘Darwins naturalisation hypothesis’ (Diez et al. 2008) which says that a species with no close relatives in a novel environment has advantages for establishment such as no direct competitors (vacant niche opportunities) and release from predators, provided the environment is suitable. Conversely a species with close relatives is more likely to find the environment suitable but opportunities for establishment are limited and survival not assured. This latter is part of ‘biotic resistance’ (Levine et al. 2004) and can prevent establishment when invasion attempts are limited, or slow the rate of invasion when attempts are sustained (Von Holle et al. 2003). Darwin’s theory implies that the degree of relatedness at species level is important but Lambdon and Hulme (2006) found no relationship with congeneric species. However in Belgium, Ricotta et al. (2010) found a positive association with the number of related species and (Strauss et al. 2006) found relationships at the family level more significant. They suggest that species specific processes are more important than relatedness. Diez et al. (2008) found no relationship with the number of congeneric species in an Auckland study but also found a negative relationship with the abundance of related species for establishment. When looking at dispersal however, Diez et al. (2008) found a positive relationship with the abundance of related plants.

The closest New Zealand relatives of *D. filix-mas* are in *Polystichum*, a genus sufficiently close to *Dryopteris* that in the Northern Hemisphere some species of each have previously been placed in the other. Three of the four native *Polystichum* are forest species although established *P. vestitum* will thrive in the open when forest is cleared and *P. richardii* does well in the increased light of a disturbed edge. *P. silvaticum* is rare and in

dense forest while the fourth species, *P. cystostegium*, occurs on open areas near and above treeline (Brownsey and Smith-Dodsworth 1989). Thus at a local scale *D. filix-mas* may experience considerable resistance to establishment by competition with established *Polystichum*. However at the landscape scale *D. filix-mas* may be well suited to occupy vacant sites, especially with degraded habitats from anthropogenic disturbance and novel habitats created by introduced woody species and exotic forests.

1.3.3 Niche Overlap

Where 2 or more species have overlapping niches there will be a central zone where they co-occur and outside this a zone where they either exclude or are excluded by the other species, often the overlap zone is where neither species thrives (Williamson 1996). An adventive organism may be able to occupy the overlap zone, displacing the indigenous species without occupying their core habitat. In species-poor systems, there may be less overlap of niches and species with similar traits, distributed on an environmental gradient may not overlap at all, potentially leaving an unoccupied niche available for exploitation. *D. filix-mas* appears to have a wide habitable range on many environmental gradients, and therefore may be able to exploit sites of overlap between various indigenous species across a wide range of natural habitats, in addition to sites that are vacant due to degradation.

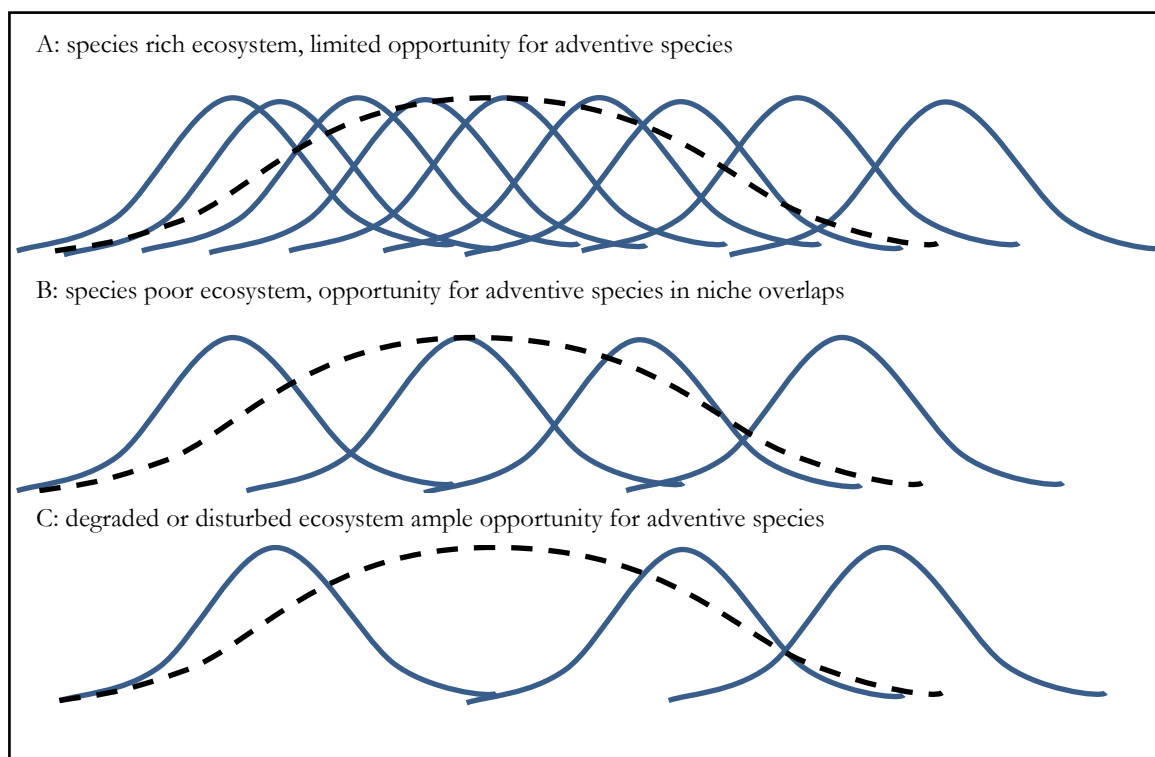


Figure 1.3 Diagrammatic representation of niche overlap. **A:** many tightly overlapping species prevent establishment of novel species. **B:** In a species poor ecosystem, species with a wide range of tolerances such as *D. filix-mas* may be able to establish in the zones of overlap. **C:** In a degraded or disturbed ecosystem some sites will be vacant facilitating easy establishment of novel species.

1.3.4 The Rule of Tens

The ‘Rule of Tens’ is put forward by Williamson (1996) largely, it seems, to drive home the point that we should not get too disturbed about most recent arrivals until we have assessed the risk that they pose. In essence the rule is that 10% (5 – 20%) of new organisms that cross a geographic border will be able to exist, 10% of these will be able to build self-sustaining populations and 10% of these will become problems. As with other rules this is not always the case and has drawn some criticism for downplaying the risk of novel organisms (Lockwood et al. 2007) but in New Zealand’s case this rule seems to be working with c. 20 000 exotic species established in 1998 and c. 240 considered to be environmental weeds (Williams and West 2000). *D. filix-mas* has achieved the first two steps, however whether it will progress to having a negative impact and therefore rate as invasive remains to be seen. Also, even if *D. filix-mas* does

prove damaging in some districts, in others it may struggle to escape from proximity to human environments, and may not warrant special attention in the face of other more imminent threats to natural habitats.

1.3.5 Propagule pressure and dispersal

D. filix-mas is wind dispersed but in New Zealand exists in a fragmented landscape where optimum sites are not continuous and may be separated by large distances. Butaye et al. (2001) studied colonisation of new woods in Belgium for numerous species. For *D. filix-mas* they found no relationship with species diversity, no relationship with patch size or with forest type. However proximity to propagule source is moderately important. They found a constant (straight) decline in probability of occurrence with increasing distance: probability was 70% in an adjoining forest declining to 20% with a 650m separation. At this point a curve develops reaching 10% at 1000m and if projected might require considerable distance (>10km) to approach 0%. As a comparison lady fern, *Athyrium filix-femina*, was highly unlikely to occur in a new forest more than 200m from an old forest. Comparing this with Otamahua/Quail Island where *D. filix-mas* continues to arrive, effective dispersal distances may be somewhat larger either because spores are dispersed further in Canterbury's windy climate or very few spores are required to successfully disperse to a suitable degraded habitat.

1.3.6 Disturbance

Causes and effects of disturbance

Disturbance may result from natural events such as the death of a tree, storm damage, landslide and natural fluctuations in community composition, or from anthropogenic sources which in New Zealand include physical disturbance, novel herbivores (mammals and invertebrates) and novel plants that alter community structure and composition, affect soil fertility and nutrient cycling.

Disturbance assists invasion (Hobbs and Huenneke 1992, Penuelas et al. 2010) as does grazing (Hobbs and Huenneke 1992, Kimball and Schiffman 2003) and raised nutrient levels, especially nitrogen and phosphorous (Penuelas et al. 2010). Biotic resistance in the form of competition may be removed by grazing e.g. cattle eat *Polystichum* spp. (pers. obs.) but may do no more than sample *D. filix-mas* as it contains toxins which have caused poisoning (Macleod et al. 1978, Mitchell and Wain 1983). *D. filix-mas* is not

listed in 'The Poisonous Plants in New Zealand' (Connor 1992) or on the Landcare Research poisonous plants website (Landcare_Research 2010). In New Zealand livestock remove groundcover from indigenous forest, increase available nutrients, alter nutrient cycles and in time open the canopy allowing more light to reach the ground. Consequently *D. filix-mas* is more likely to occur in recently grazed forest remnants than forests that have not been grazed, and may have an advantage over native species when grazing is removed.

Compaction

Much of New Zealand's hill soils are yellow-brown and yellow-grey earths dominated by loams which in undisturbed sites tend to have an open, nutty structure. Cultivation breaks down the structure making soil vulnerable to compaction while grazing mammals compact soil, impeding root and moisture penetration, which may negatively affect the establishment of indigenous forest species. Godefroid and Koedam (2004) studied the effect of soil compaction on forest herb distribution. While many species had optimum soil densities, there was no significant relationship for *D. filix-mas* although *Dryopteris dilatata* had a narrow optimum range of 150 – 450 Newtons, by comparison the occurrence of *Deschampsia caespitosa* (a tussock grass) was increasing at the maximum force presented (1200N). In support of this Roovers et al. (2004) found that *D. filix-mas* was neither more nor less likely to colonise forest paths while *Deschampsia caespitosa* is a preferential coloniser of paths.

Post-disturbance regeneration

'Bottle' experiments demonstrate that the order in which organisms colonise a new habitat has a long-term effect on the make-up of the resultant community (Drake 1991, Price and Morin 2004). If *D. filix-mas* is able to dominate degraded habitats following removal of disturbance e.g. previously grazed forest remnants, it may alter successional trajectories and may prove difficult to eliminate. Also, if *D. filix-mas* is better able to colonise physically disturbed sites than native ferns and forbs, maintaining low propagule pressure in relatively pristine areas may become important.

Lag times

Lag times between establishment of an organism, its dispersal and its being regarded as invasive can have several causes. In the case of *D. filix-mas* these are likely to include:

- conditions for effective wider dispersal being met infrequently, for example wilding pines only achieve mass long distance dispersal at infrequent intervals (Ledgard 2001).
- In order to disperse from a town or city *D. filix-mas* may need to cross a considerable width of intensively managed horticultural and agricultural land to reach sites suitable for mature plants to develop.
- Observer bias may give the impression of a sudden spread or increase where awareness of *D. filix-mas* comes as the population reaches a certain density. Dispersal to a given locality may take some time and only when the second or third generation become established does it become noticeable.

Table 1: The fit between *Dryopteris filix-mas* and selected indicators of invasiveness.

| Indicators for a potentially invasive plant | Applies to <i>D. filix-mas</i> | Comments |
|---|--------------------------------|--|
| Higher photosynthetic potential : dry mass ¹ | Unknown | Not measured |
| Higher leaf area: leaf mass ¹ | Yes | Pinnæ are thin |
| Higher mineral concentrations ¹ | Unknown | Advantage not shown |
| Related to natives ² | Yes | There are several native genera in Dryopteridaceae with <i>Polystichum</i> sufficiently close that the two genera have been confused in Europe. Relatedness works at the landscape scale but at local scale abundance of related plants limits invasion. ³ However abundance of related plants is positively correlated with spread following establishment. ³ |
| Phenotypic similarity ² | Yes | A number of NZ ferns have a similar size and habit. |
| Biotic resistance | Unknown | Competition likely in natural habitats but less likely in degraded habitats |
| High propagule pressure ⁴ | Yes | Numerous spores dispersed widely in autumn and winter, ample wind in NZ. |
| Habitat suitability ⁴ | Yes | A wide range of habitats in its natural range; the suitability of parts of New Zealand has been demonstrated |
| Previous invasion success | Yes | Originated in Mediterranean area and dispersed across entire northern hemisphere temperate zone. |
| Allelopathic | Yes | Gametophytes can prevent neighbouring gametophytes developing archegonia. An inter-species effect may or may not occur with <i>D. filix-mas</i> . |
| Jump dispersal and fat-tailed dispersal ⁵ | Probable | No known studies for <i>D. filix-mas</i> see Butaye et al. (2001) for implied dispersal patterns |
| Soil compaction | Yes | Farm animals cause severe surface compaction of farm soils which may be detrimental for native ferns but <i>D. filix-mas</i> appears unaffected by compaction. |
| Disturbance | Yes | a) <i>D. filix-mas</i> tolerates disturbance and may even capitalise on it. b) High levels of disturbance in environment: exotic forestry, grazing, introduced mammals. |
| Mycorrhizal independence | Yes | <i>D. filix-mas</i> forms mycorrhizal associations with generalist mycorrhiza but does well in most situations without. |

1 Penuelas et al. 2010; 2 Ricotta et al. 2010; 3 Diez et al. 2008; 4 Williamson 1996; 5 Lockwood et al. 2007;

1.4 Thesis goals and approach

This study will begin the process of gaining an understanding of the ecology of *D. filix-mas* in New Zealand; how it interacts with native species and whether the observed spread through degraded indigenous habitats in Canterbury is cause for concern with regard to intact indigenous habitats. Specifically, this research will address the following questions:

1. What are the habitat requirements for *D. filix-mas* in rural North Canterbury and which indigenous plants share those habitats?
2. Does *D. filix-mas* preferentially occupy novel habitats (degraded sites and exotic dominated plant communities)?
3. What levels of light/shade are conducive to the growth of *D. filix-mas*?
4. What is the current distribution of *D. filix-mas* across New Zealand and from this can we predict where *D. filix-mas* is likely to occur in the future?

These research questions will be addressed by the following approaches:

1. Field collection of empirical data, from a range of habitats in the wider North Canterbury region including abiotic parameters and associated species. Where practical, adjacent degraded and protected habitats will be sampled.
2. Habitat preference data will be collected in conjunction with approach one above.
3. A controlled environment experiment of light and shade requirements.
4. GIS application using all confirmed records available and the Land Environments New Zealand (LENZ) dataset to examine where *D. filix-mas* is likely to be successful given the environmental information currently available and collected in this study.

2 Chapter 2 Effects of light environment on growth of *D. filix-mas*

2.1 Introduction

The shade and light requirements for *D. filix-mas* are not fully understood. In the Northern Hemisphere *D. filix-mas* plants occur in light to heavy shade under deciduous woods where ferns experience high light in the spring (Ash and Barkham 1976; Pigott and Taylor 1964). However, how this compares to the situation in evergreen broadleaved forest conditions is not clear from the available literature.

A number of studies with ferns under different light conditions can be found and the most relevant was a New Zealand study of wild ferns, looking at three native species and *D. filix-mas* (Bannister and Wildish, 1982). Shade grown plants, irrespective of species, had higher specific leaf areas and specific leaf area was negatively correlated with the light compensation point. In another study the positive relationship between phenotypic plasticity and tolerance to a range of light conditions was demonstrated with *Blechnum* spp. (Saldaña et al. 2005). In addition, Kawai et al. (2003) found that *D. filix-mas* is phototropic under red-light, a trait considered to be an adaptation to low light conditions.

Related studies include the growing of gametophytes of three species of *Dryopteris* under different light conditions with photosynthetically active radiation (PAR) of 40µmols to 2.5µmols (Jiménez and Quintanilla 2009). One of the subjects was *D. oreades* a reputed parent of the hybrid from which *D. filix-mas* originated (Fraser-Jenkins 1986).

Gametophytes formed and grew under all light conditions with proportionally more female gametophytes under low light; unfortunately the experiment was terminated without evaluating success in sporophyte development. A shade experiment with ferns found that species associated with shady sites had lower light compensation points and lower light saturation points (Ludlow and Wolf 1975).

This chapter tests the hypotheses 1) that *D. filix-mas* has optimum levels of shade and light for growth and 2) the likelihood that the low light levels in New Zealand indigenous evergreen forests will be sufficient for *D. filix-mas* to establish and grow successfully.

2.2 Method

2.2.1 Design and establishment

In this experiment the effects of four light levels on the growth of *D. filix-mas* was assessed in a fully replicated trial undertaken at the University of Canterbury, from December 2010 through to mid-May in 2011. The trial involved growing five plants of *D. filix-mas* per replicate, with space constraints at the experimental site limiting the experiment to eight replicates per treatment. The experiment was laid out in four rows, with replicates of each treatment randomly assigned to each row. Wet pot weight measurements (Morgan and Norton 1992) were made in January and May. Rhizomes were weighed in December and all plant parts were weighed fresh at the end of May and again when dried.

To limit opportunity for genetic variation, dormant rhizomes were collected from a 100m radius area in a QEII Covenant in the Blythe Valley, North Canterbury in late winter. However this resulted in considerable variation in rhizome size and maturity and with concern over having unequal effects from transplant shock, five plants were used in each replicate to average out any extreme effects from transplant shock and size difference.

Rhizomes were visually sorted into seven sizes and weighed using a calibrated Ohaus Navigator 410 balance with 0.01gm accuracy; this balance was used for all weight measurements at the end of the experiment. Rhizomes were kept in a cool store and potted into PB5 bags in late November using a standard commercial potting mix. Potted ferns were then placed into a semi-shaded site for two weeks to establish. The smallest and largest rhizomes were separated, leaving five groups of rhizomes to use in the experiment and a pool of plants in reserve if needed. At the end of the two-week establishment period, plants were placed consecutively into the treatment replicates, starting with the smallest group of rhizomes but with no further sorting, i.e. the plants in each size group were distributed randomly across all replicates. Plants that showed signs of stress or were not doing well were not used. This resulted in a few of the small and large plants previously set aside being used to ensure that there were sufficient plants in each replicate. In order to control for loss of potting mix weight through

oxidation, leaching and physical transport, an additional pot was placed in each replicate containing potting mix only and weighed at the same time as the pots with plants.

Treatments were assigned to each replicate using a random number table resulting in the layout in figure 2.1 below. Pots were clustered at the centre of each space with

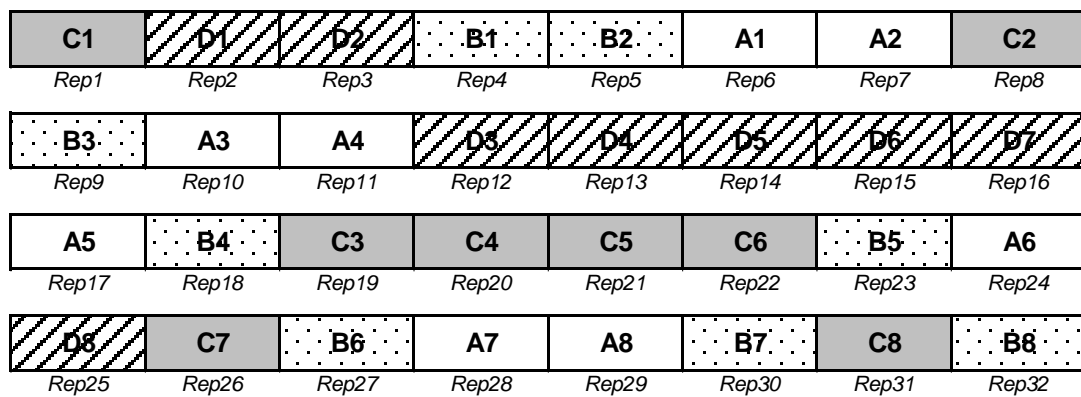


Figure 2.1 Layout of replicates in the study area. A: full exposure, B: single layer of shade cloth, C: double layer of shade cloth, D: triple layer of shade cloth.

approximately 1m between replicates.



Figure 2.2 experiment layout and pot arrangement. View from replicate 8 (near left) to replicate 25 (centre distance)

Permathene Heavy Shadecloth (73% shade) was laid over Kerilea cloche hoops (1.0m wide) in 1, 2, or 3 layers as necessary, with the cloth being extended to the ground, within the row, between treatment levels. To ensure plants did not suffer water stress from lack of water availability, pots were watered daily with automatic drippers and additional sprinklers were used over the fully exposed pots (Treatment A).

2.2.2 Light levels

PAR was measured between 1pm and 2.30pm on three days at the beginning of April using four LiCor 190 Quantum sensors, each sensor was assigned to one treatment, and the output was recorded with a Campbell Scientific CR10X datalogger. Simultaneous measurements were taken in the centre of each replicate at a site, and this was repeated at each of four sites on each day, see fig.2.2.3 for layout. The datalogger was set to average readings every five minutes, and managed, so as to obtain an uninterrupted record for 10 minutes at each site on each day. One day was cloud free, one in full sun with scattered clouds and the other in bright but overcast conditions. The latter is a common situation in Christchurch, potentially reducing the effects of direct shading and any effects that are artefacts of the experiment layout (row orientation, hoop shadows, folds in the shadecloth etc). The four sampling sites were chosen to accommodate the limitations of the equipment (cable length).

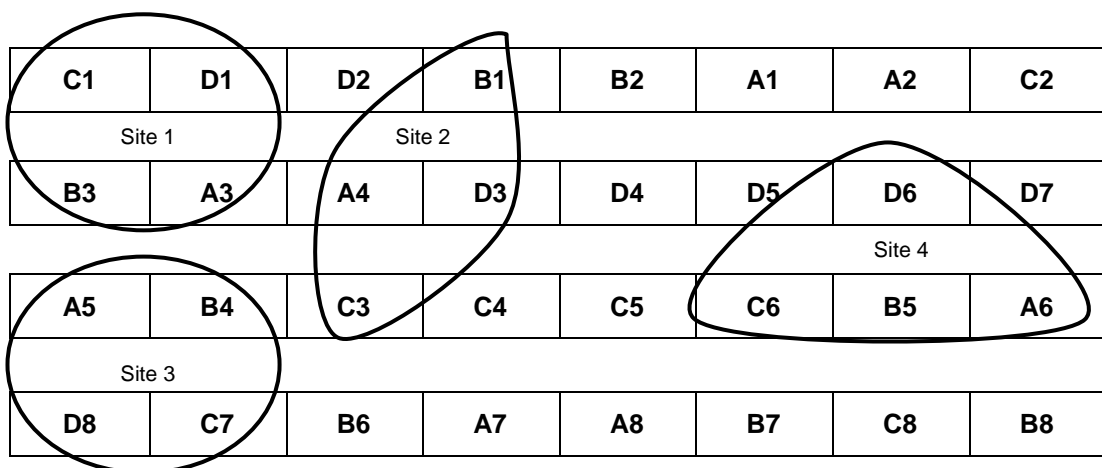


Figure 2.3 Replicate groups used to obtain light level measurements

2.2.3 Wet Pot Weights

Wet pot weights were taken in the first week of January after the plants had fully unfurled their first fronds and the final measurement was taken at the end of the experiment in May. The wet pot method (Morgan and Norton 1992) requires weighing the plant and pot when the plants are fully turgid and the potting mix is at field capacity. In practice this proved to be somewhat difficult in a summertime field environment. In a controlled environment pots would be soaked for several hours (to a saturated state) and then drained until all dripping stops (c. 24hrs) at which point it is presumed that remaining water is held within the soil, either absorbed into organic matter or prevented from draining by capillary action but this method proved impractical and required modification.

The bark-based potting mix was kept in a moist state by daily watering which seemed to have the effect of reducing the need for prolonged soaking. A trial was conducted with a few spare pots in which it was found that no measurable weight gain was achieved with further soaking beyond one hour. Observation during the same trial showed that in the hot conditions for the initial measurements the top of the bark potting mix was starting to dry after only a half hour of draining. In response to this, draining for a half hour, followed by placement on a towel for five minutes (to draw out excess water) produced moderately consistent weights.

From this, the method for obtaining wet pot weights became a one hour minimum soak, followed by a half hour drain and a further five minutes resting on a towel before weighing. Weights were obtained with a set of Salter electronic scales with a nominal accuracy of 1gm.

2.2.4 Plant Weights

At the completion of the experiment plants were harvested. Fronds were removed, placed in zip lock bags and weighed. They were then transferred to paper bags and placed in a Contherm Cat. 260 General Purpose Oven at 80°C for 48hrs to dry followed by placement in a desiccator to cool, from which they were taken individually and weighed; noticeable weight gain from atmospheric moisture began after c. 5 seconds out of the desiccator. Once the fronds were weighed, the empty paper bags were replaced in the drying oven overnight and the weighing procedure repeated. Fresh weight is the

measured fresh weight of the sample less the weight of the zip lock bag and dry weight is the measured dry weight less the paper bag weight.

Rhizomes were removed from their pots and washed as carefully as possible over a sieve to avoid root loss and minimise retention of bark and fertiliser pellets. They were then wrapped in paper towels (to keep roots intact), placed in individual cloth bags and spun in a domestic washing machine followed by blotting with paper towels to remove excess water. Weighing and drying was the same as for fronds, except that fresh weights were obtained directly and drying continued until a sample of the largest rhizomes at different locations in the oven had ceased losing weight.

2.2.5 Statistical analyses

For analysis the measurements obtained from the five plants in each replicate were combined and averaged to give single values for each variable in each replicate.

Initial data processing was carried out in a Microsoft Excel spreadsheet, including the calculation of the ratio of dry weight to fresh weight. The calculation of percentage change in fresh weight for rhizomes, and statistical tests were conducted with the “R” statistical package versions 2.10.0 – 3.0.2 (R Core Team, 2013) with plots and graphs also being produced in “R”.

For wet pot weight the percentage change in weight was first calculated, and then analysed with Analysis of variance (Anova) after which Tukey’s Honest Significant Differences Test (Tukey HSD) was applied.

Start weights were analysed with a one-way Anova to check for undue variation in the distribution of rhizomes between treatments. A summary bar graph revealed a pattern of size distribution similar too, but less pronounced than what would be expected if the Null Hypothesis is false (Figure 2.6). In response to this and because plant size can influence subsequent plant growth, start weights were retained for the analysis of change in rhizome weights and the analysis of dry weights requiring the use of Analysis of co-variance (Ancova). Contrasts between treatments were then obtained in ‘R’ by the use of ‘relevel’ as tests such as Tukey HSD cannot be used.

2.3 Results

2.3.1 Losses and Damage

No plants died during the experiment, however plants in Treatment A (no shade) had most of their spring growth fronds blown off by wind as was also the case with many subsequent replacement fronds. This was not seen with exposed plants in the wild and may be exacerbated by the study ferns being in raised pots with no surrounding vegetation that would slow surface winds or directly support fronds. Wind also caused occasional damage to fronds on plants in the other treatments.

A couple of pots in Treatment A, were also found knocked over on one occasion but very little potting mix was spilled and this was mostly recovered.

2.3.2 Photosynthetically Active Radiation in each treatment

The single layer of shade-cloth excluded a mean of 69% of PAR with a range of 65 – 73%. The double layer excluded a mean of 89% of PAR with a range of 87 – 92% and the triple layer excluded a mean of 96% of PAR with a range of 94 – 98%.

Table 2.1 Photosynthetically active radiation (PAR), transmitted by the different shade cloth treatments. Percentage of PAR averaged from four replicates/treatment, repeated on three days.

| | Single layer Treatment B | Double layer Treatment C | Triple layer Treatment D |
|---|-----------------------------|-----------------------------|-----------------------------|
| Mean % PAR of all 4 sites/ treatment over all 3 days | 31.0 | 11.3 | 3.8 |
| Lowest % PAR | 26.8 | 8.6 | 2.4 |
| Highest % PAR | 34.3 | 12.7 | 5.4 |

2.3.3 Wet pot weight change

The shade treatments had a significant effect on change in wet pot weight ($P = 0.016$). Further analysis with Tukey HSD shows that with the wet pot method as applied here, the difference between treatments B and D is highly significant with an adjusted P value of 0.009; treatment B resulting in a greater weight gain than treatment D. No other treatment comparison has a significant difference.

Table 2.2 Significance (P) values for change in wet pot weight from Tukey's Honest Significant Differences Test. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

| Treatments compared | Adjusted P-value |
|---------------------|------------------|
| C-D | 0.543 |
| A-D | 0.441 |
| B-D | 0.009** |
| A-C | 0.998 |
| B-C | 0.171 |
| B-A | 0.231 |

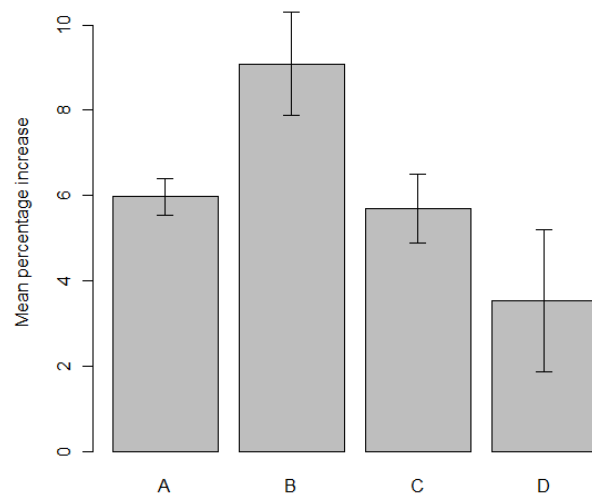


Figure 2.4 Wetpot mean percentage increase with CI ± 1 s.e. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

2.3.4 Start weights of rhizomes

Initial analysis of results revealed that replicate 29 had increased in weight disproportionately to the remaining replicates in the same treatment (treatment A: no shade) and may have an undue effect on the analysis (Figure 2.5 below). Replicates 29 - 32 were adjacent to a storage container (visible in Figure 2. 2, page 21), which shaded

this area of the experiment on sunny afternoons during the hottest months. Replicates 30 – 32 (treatments B and C) were not noticeably influenced by this additional shading. As a result, replicate 29 was removed for the analysis but replicates 30 – 32 were retained.

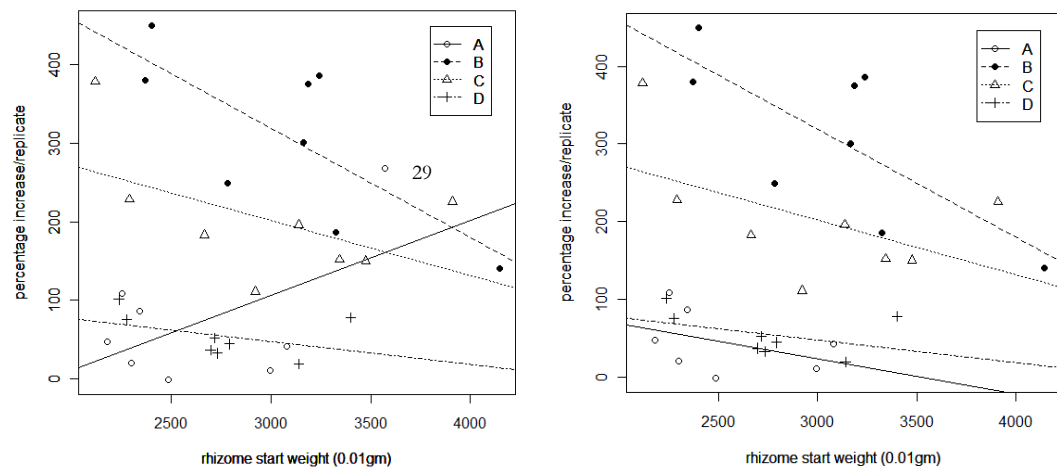


Figure 2.5 Regression lines for start weights~percentage increase, by treatment, with (top) and without replicate 29 (Treatment A: no shade), which was shaded by an adjacent structure during summer afternoons. A: no shade; B: single shadedcloth; C: double shadedcloth; D: triple shadedcloth.

Having removed replicate 29, initial rhizome weights (replicate average) were tested for significant differences in the allocation of rhizomes between treatments. This showed that the differences between treatments is not significant ($P=0.1594$).

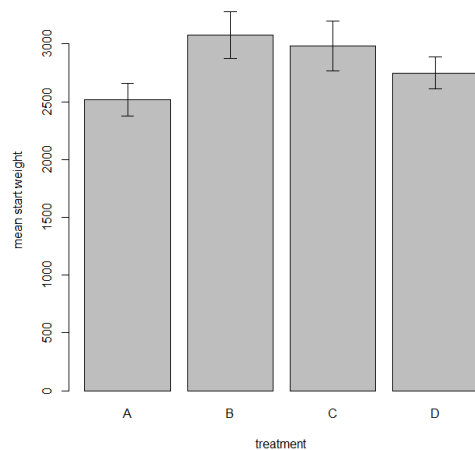


Figure 2.6 bar graph of mean rhizome start weight by treatment with replicate 29 removed. CI is 1 s.e. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

2.3.5 rhizome and roots, fresh weight change

The combined fresh weight of rhizomes and roots was assessed as percentage change (increase from start weight) and while the analysis of start weights in section 2.3.3 indicated that differences in start weight were not significant, start weight was retained as a covariable following the precautionary approach recommended in Crawley (2005).

While the interaction of treatment with start weight (differences between slopes) is not significant ($P=0.376$), treatment is significant ($P<0.001$) and start weight itself is also significant ($P=0.001$) Figure 2.7 shows this relationship, where the Ancova has computed a single slope (-0.0839) because only the differences between intercepts are significant.

Treatment B (69% shade) had the greatest increase in fresh weight (approximately 308%), followed by Treatment C (89% shade) at approximately 203% increase, while Treatments A (full exposure) and D (96% shade) were similar having approximately 45% and 55% increase in weight, respectively.

The only treatments that are not significantly different from each other are A and D. Reordering the treatments with 'relevel' showed that differences with all other treatments are very highly significant ($P\leq 0.001$) as shown in Table 2.3.

Table 2.3 Comparison co-efficients for percentage change in fresh weight with start weight as a co-variable. Adjusted R-squared: 0.79; F-statistic: 28.47 on 4 and 26 DF; overall p-value: 3.657e-09 A: no shade; B: single shadedcloth; C: double shadedcloth; D: triple shadedcloth.

| Treatment | Estimate | Std. Error | t value | Pr(> t) |
|-----------|------------|------------|---------|--------------|
| A-B | -309.95780 | 33.93708 | -9.133 | 1.35e-09 *** |
| A-C | -196.83365 | 33.16468 | -5.935 | 2.91e-06 *** |
| A-D | -29.50307 | 31.80505 | -0.928 | 0.3621 |
| B-C | -113.12414 | 30.36437 | -3.726 | 0.001 *** |
| B-D | -280.45473 | 31.23337 | -8.979 | 1.90e-09 *** |
| C-D | -167.33059 | 30.77403 | -5.437 | 1.06e-05 *** |

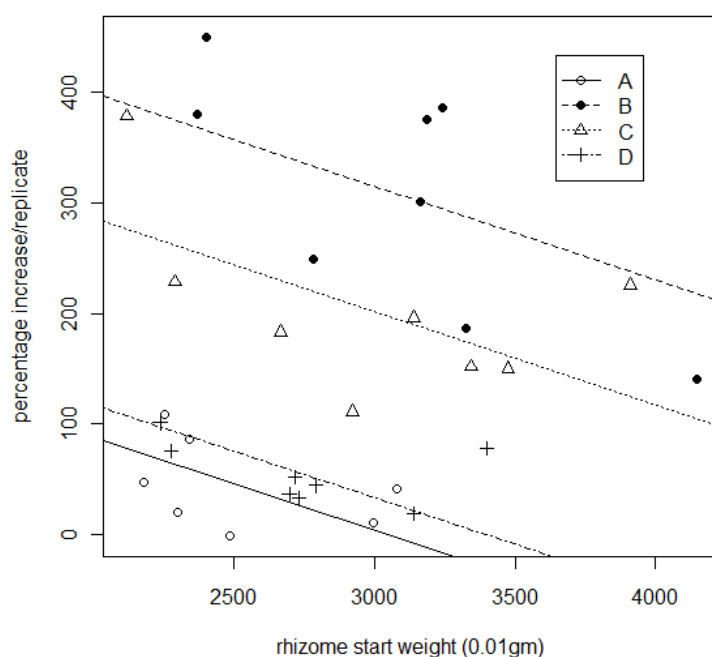


Figure 2.7 Regression for percentage increase in rhizome fresh weight. Slope = -0.0839 from Ancova with rhizome start weight as an additive covariable. A: no shade; B: single shadedcloth; C: double shadedcloth; D: triple shadedcloth.

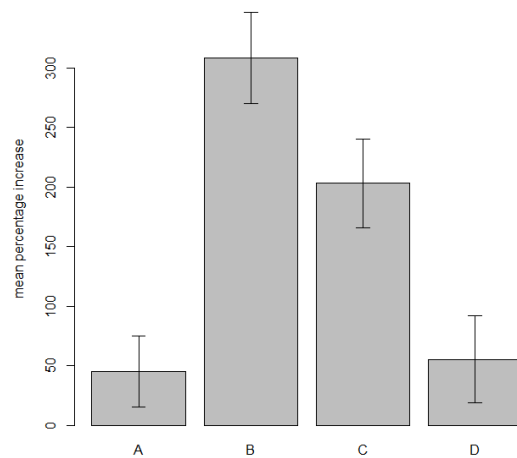


Figure 2.8 Mean % increase/treatment (A n=7,B:D n=8) with ± 1 s.e. for “treatment + start weight” as explanatory variables. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

2.3.6 Whole plant dry weight

Analysis of co-variance showed that treatment is very highly significant ($P \leq 0.001$) and start weight is not significant ($P = 0.0534$).

One way anova then showed that treatment is responsible for 90% of the variation explained ($R^2 = 0.899$) and Tukey HSD showed that all treatments have very highly significant differences with the exception of the contrast between A and D ($P = 0.3111$) in Table 2.4

Table 2.4 Tukey HSD test results for shade treatments with whole plant dry weight. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

| Treatment comparison | P adjusted |
|----------------------|------------|
| A-B | 0.0000 |
| A-C | 0.0000 |
| A-D | 0.3111 |
| B-C | 0.0001 |
| B-D | 0.0000 |
| D-C | 0.0000 |

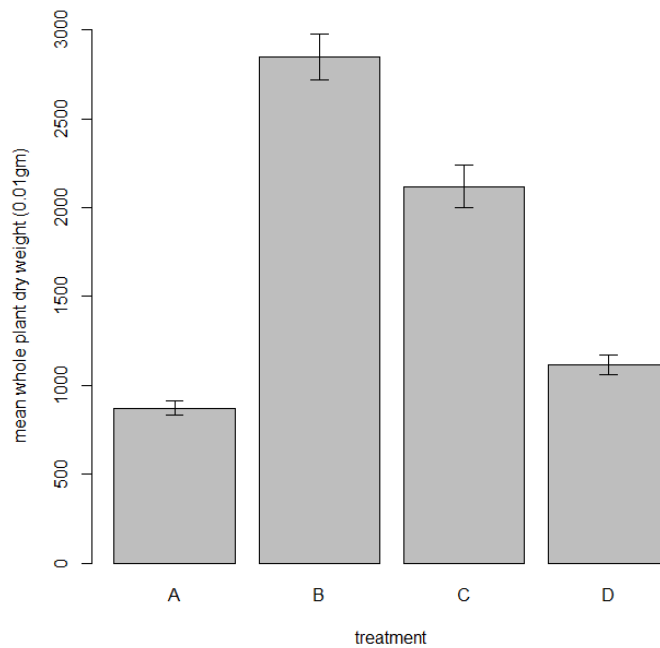


Figure 2.9 Mean total dry weight by treatment (A n=7,B:D n=8) with ± 1 s.e. for “treatment + start weight” as explanatory variables. A: no shade; B: single shade cloth; C: double shade cloth; D: triple shade cloth.

2.4 Discussion

This experiment has demonstrated that established plants of *D. filix-mas* grow best under a light regime somewhere between full all-day exposure to sunlight and 89% shade. It has also demonstrated that *D. filix-mas* is unlikely to be shaded out by a dense canopy as plants gained in mass under the heaviest shade treatment (96 % shade) although light in New Zealand forests is often as low as 2% of PAR (98% shade) (Kelly and Skipworth 1984; McDonald and Norton 1992; Ebbett and Ogden 1998; Lusk et al. 2009). Although plants gained in weight under all treatments this does not mean that *D. filix-mas* will successfully establish across this full range of light exposure. In the first instance the experiment eliminated water stress in the fully exposed sites by maintaining pots in a moist state. Secondly, nothing can be inferred from this experiment about the conditions required for successful establishment of a *D. filix-mas* sporophyte from spores and thirdly Treatment A (full light) was in fact full exposure to light and wind with excess heat.

In all measures tested, treatment B (single layer of shade cloth providing c. 69% shade), had the highest growth. It is tempting to suggest that this is near to the optimum level of shade but field observations of large robust plants in fully exposed sites would suggest that the optimum light levels may lie much nearer to full sunlight or to sites that get full sunlight for part of the day. Equally the optimum may be under heavier shade than 69% although there is a clear decline in growth at 89% shade. The only certainty is that the optimum lies between full sunlight and 89% shade.

Under treatment D (3 layers of shade cloth providing c. 96% shade), the increase in fresh mass by approximately 50% suggests that established *D. filix-mas* can successfully tolerate heavier shade, although how comparable triple shade cloth is to the forest floor under a dense canopy is unclear. In low light conditions sunflecks can be major contributors to PAR on the forest floor (McDonald and Norton, 1992; Coomes et al., 2005; Skre et al. 1983) and dull overcast conditions can result in increased PAR at the forest floor relative to PAR on sunny days (Chazdon 1988). While fully exposed plants in treatment A had similar changes in weight to plants in treatment D, resulting in differences between them being not significant, it cannot be said that fully exposed plants performed poorly due to the intensity of sunlight. These fully exposed ferns were subjected to an unnatural level of heat in black pots on a black surface. Perched approximately 150mm up into the air and wind they lost their first set of fronds to wind, most then failed to replace these with full sets and many replacement fronds were also broken off. Therefore their poor performance compared to treatment B may rather be due to other factors than an intolerance of full sunlight.

This study supports the findings of Bannister and Wildish (1982) who found that the four ferns they studied (including *D. filix-mas*) were "...well adapted to a range of light intensities." They also noted that as specific leaf area increased, the light compensation point dropped and with lower temperature the light compensation point for *D. filix-mas* fell to 18lux at 8°C compared to 55lux at 24°C indicating that plants in deep shade (cool sites) are able to balance respiration and photosynthesis in low light conditions. This would have some bearing on the plants ability to increase in fresh mass under all treatments in this study.

The wet pot method was less than ideal for this study due to the difficulties with obtaining field capacity in the pots as mentioned in methods, and also due to weighing ferns in a field situation where wind caused fluctuations up to 50gm on the scales during measurement. Fronds acted something like a balloon, rising and falling with fluctuations in local air pressure. This approach would however be useful in a fully enclosed situation where drying of the potting mix surface can be prevented while the pot drains to field capacity.

This study may have benefited from some interspersions in the design e.g. having two plots from each treatment in each row and from testing the distribution of rhizomes before they were placed into the treatments, providing opportunity to be more rigorous in the stratification of rhizome sizes across the treatments and replicates if necessary. Further studies to build on this work would be to narrow down the optimum light conditions for *D. filix-mas*, and to conduct trials with propagation from spores under different light and moisture regimes with similar field experiments in indigenous forest, that could also test for propagule pressure limitations.

Plant plasticity was not directly studied in this experiment. However second flush fronds from Treatments A and B appeared to be proportionally shorter but were noticeably coriaceous, while in Treatment C fronds were large and thin and in Treatment D fronds were smaller, thin and weak. The changes in frond dimensions and thickness were quite noticeable (see figure 2.4.1) supporting the idea that ferns with high phenotypic plasticity are tolerant of a wider range of light conditions (Bannister and Wildish 1982, Liao et al. 2013).



Figure 2.10 Effects of treatments on frond form: Each column is 1 replicate, left to right Treatment D, 4% PAR, small thin fronds; Treatment C, 11% PAR, large thin fronds; Treatment B, 31% PAR, large, coriaceous fronds; Treatment A, no shade (100% PAR), small coriaceous fronds.

3 Chapter 3 Male fern habitat preferences in North Canterbury

3.1 Introduction

D. filix-mas is widespread in North Canterbury from suburban sections and ruderal sites to waste land, shelter belts, streamsides, forest plantations and habitats dominated by indigenous species. However, quantitative descriptive data are lacking. This chapter describes the field work undertaken. Presents the results from the ordinations and statistical analyses used to examine the data collected, and discusses the results with reference to the research questions.

This Chapter seeks to fill some of the lack of quantitative data exploring the following questions previously outlined in Chapter 1. The first is to identify the habitat requirements for *D. filix-mas* and the plant species that share those habitats. Second, to ask if *D. filix-mas* is preferentially associated with novel habitats compared to natural indigenous habitats. Third is to determine whether or not *D. filix-mas* is invasive and, if so, can habitats at risk be identified? The fourth question relates to light requirements and while this is addressed by Chapter 2, relevant field data for the light preferences of *D. filix-mas*, will be collected.

The null hypothesis for this part of the study is that *D. filix-mas* will not have any demonstrable preferences for where it grows in the North Canterbury landscape; and further, where it grows will not be correlated with any other plant species or with vegetation types.

3.2 Study Sites

Study sites were located through North Canterbury, New Zealand from the Rakaia River in the south to the Mandamus River in the north with a lowland coastal site, foothills sites and two inland sites. Most sites were on private property (farms and exotic forestry) with two sites administered by the Dept. of Conservation. Several sites were found with the assistance of the Queen Elizabeth II National Trust (QEII Trust). The local QEII Trust representative (Miles Giller) identified potential private covenants through his knowledge of the covenants and made initial contacts with property owners before passing on contact details.

The original intent had been to find a number of sites where different land managements could be compared side by side. This proved impractical as most sites were either too small or *D. filix-mas* too scarce to gain meaningful data. Consequently inland and foothills sites were combined into one dataset for analysis as individual sites had insufficient data for stand-alone analysis. This data was also separated into plantation and indigenous sites, as the exotic conifers dominated the ordinations. The coastal site of Tiromoana Bush provided the best set of data with sufficient plots for analysis in isolation from the other sites.

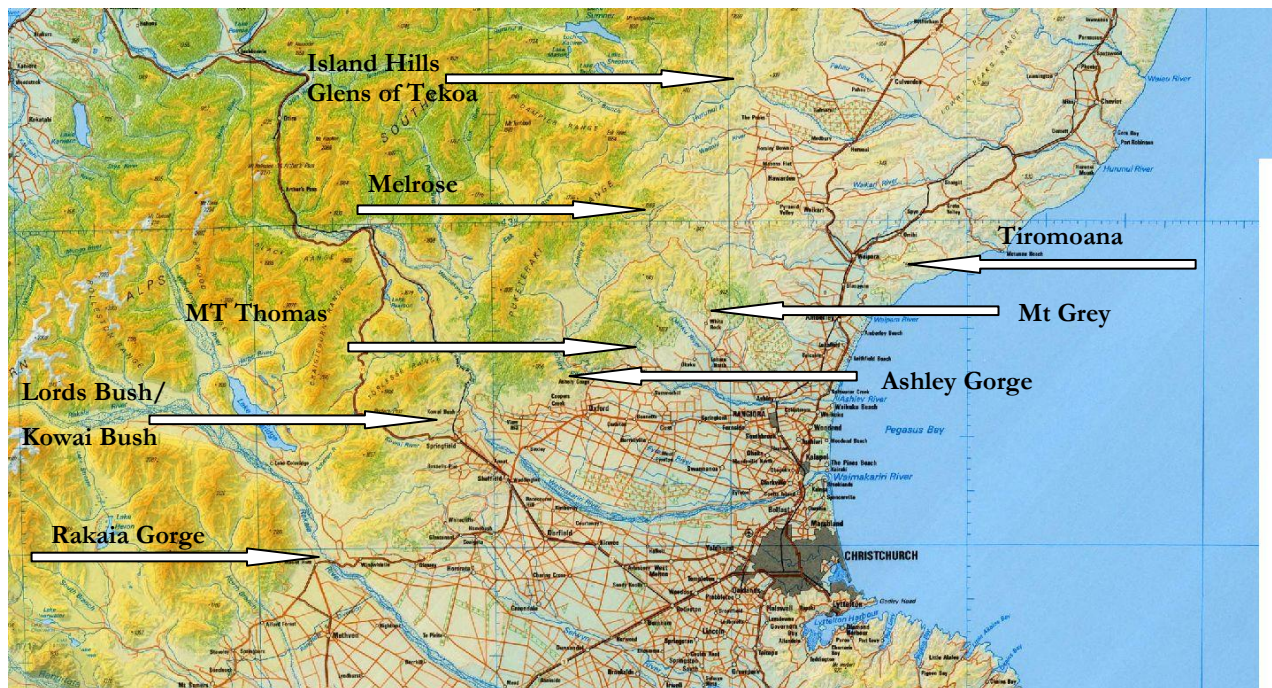


Figure 3.1 Map of North Canterbury with study sites indicated.

3.2.1 Tiromoana Bush

Tiromoana Bush is part of a recently retired farm that has been covenanted under the QEII Trust and had a walkway developed as part of the Kate Valley waste management - landfill operated by TransWaste, Canterbury Ltd. Canterbury University has several ongoing studies around restoration and regeneration at the site under The School of Forestry and this was the only site where a thorough survey was practical.

Tiromoana Bush is comprised of several remnants of second growth, indigenous forest of various ages and on a range of aspects. The majority of these forests occur either in the central gorge that divides the Covenant on approximately an east – west axis or on

the south facing slopes in the northern part of the Covenant. Due to safety considerations the gorge area was avoided during field work, instead focussing on the gentler upper slopes.

With the exception of some gullies leading into the gorge, forest is dominated by a continuous canopy of kanuka (*Kunzea ericoides*) of various aged stands reflecting a history of periodic burning. Kanuka is a seral species that initially blocks light, drops a heavy rain of litter and dries the soil precluding an understorey. As it matures groundcover and understorey species gradually move in with shade tolerant forest species eventually replacing the kanuka when the canopy collapses in senescence. Undergrowth patterns at Tiromoana are also affected by grazing history which is reflected in the, at times, almost impenetrable undergrowth of the unpalatable divaricating shrubs *Coprosma rhamnoides* and *Helichrysum lanceolatum*.

The underlying geology is primarily sedimentary in origin, with hard limestone, soft sandstone and calcareous mudstone, these are overlain in places with loess derived soils, and are generally described under Stoneyhurst Hill Soils (Norton 2005). The plots covered in this survey were mostly on loess derived soils with occasional outcroppings of limestone, although high levels of calcium were indicated by the common presence of the obligate calcicole fern, *Asplenium lyallii*.

Tiromoana Bush has climatic conditions that are clearly distinct from inland areas being relatively sheltered from the effects of the infamous foehn wind “The Nor-wester” and prone to prolonged periods of mist and drizzle during what is otherwise fine weather conditions. The east aspect and exposure to the sea also moderates the extremes of winter as demonstrated by the presence of cold sensitive kawakawa, *Macropiper excelsum*, and ngaio, *Myoporum laetum*. Reported rainfall for Kate Valley is an average of 921mm (Norton, 2005) although an isohyet map in Chater (2002), suggests this may be over 1200mm in the north eastern study area due to orographic effects from the Mt Cass escarpment 3km to the north.



Figure 3.2 An oblique view of the Tiromoana Bush study area viewed from the south with GPS plot points marked. Kate Valley drains through the bluffed gorge to the right (Image from Google Earth, 11 June 2010).

Variation to plot layout

Plots in the southern remnant (foreground in Figure 3.2) were spaced at 25m with transects 100m apart due to the narrow nature of this remnant and to better sample the narrow ravine, while retaining the same number of plots/ha.

3.2.2 North Canterbury Foothills and inland sites

Four sites were visited along the Canterbury Plains foothills: Rakaia Gorge; Kowai Bush and Lords Bush; Mt Thomas and Mt Grey. Three additional inland sites between the Ashley River and Wairau were also visited: Melrose, Glens of Tekoa and Island Hills Stations.

Rainfall in Canterbury is most strongly correlated with altitude(Chater 2002) increasing steadily with altitude such that estimates of rainfall, for foothills and inland sites lie between 900 and 1100mm. Rainfall at inland sites is less than might be expected but may experience steep gradients on hillsides and also experience some rain-shadow

effects with weather from all directions. However Melrose at 457m a.s.l. has a 50yr mean of 964mm and from the same data Mandamus (Glens of Tekoa and Island Hills Stations) at 300m had 950mm. Mt Grey is estimated to receive from 800mm at its base around 150m a.s.l., to 1200mm at its 930m summit (Chater 2002). Soils range from yellow-grey earths at the lower rainfall to yellow-brown earths at the higher rainfall, and are generally derived from greywacke bedrock, alluvium, talus, loess or an admixture of these. However at Raikaia Gorge there are basaltic soils derived from Mt Somers volcanics.

Foothills

Rakaia Gorge

The Rakaia Gorge Walkway traverses the lower gorge on the true left (north) bank travelling upstream from State Highway 77. At this point the Rakaia River has cut through Mt Somers volcanics to form a precipitous and serpentine gorge. The soils are consequently derived from a mixture of greywacke alluvium and basic igneous rocks providing for a slightly different flora, e.g. fierce lancewood (*Psuedopanax ferox*). *D. filix-mas* is relatively abundant in admixture with *D. affinis*, and on soils derived from the igneous rocks there is an extensive population of *D. x tavellii*. *Cotoneaster* (*Cotoneaster simonsii*), and broom (*Cytisus scoparius*) are common brush-weeds.

The topography of the gorge proved to be too rugged for proper transects with only one short compass transect through a ravine being feasible. As a result the walking path was used as a primary transect with plots at random distances into the vegetation on alternating sides of the path extending into short transects when the terrain was suitable.

Kowai Bush and Lords Bush

Kowai Bush is a tiny private reserve near Springfield on a rolling hill that runs down onto flat land where Lords Bush Scenic Reserve is located 500m across paddocks. Soils at both sites are derived from greywacke overlain by loess but where the former is mostly well-drained and dominated by black beech (*Fuscopora solandri*) the latter is poorly-drained and is the last intact remnant of podocarp forest on the upper plains. Lords Bush is dominated by kahikatea (*Dacrycarpus dacrydioides*) in association with pokaka (*Elaeocarpus hookerianus*). Both sites have been disturbed by grazing and partial

logging and both are rather small limiting the capacity for transects in the prescribed manner.

A single transect was made at each site and additional plots were added to record the situations in which *D. filix-mas* was found.

Mt Thomas



Figure 3.3 Mt Thomas plots from the east, pale forest is Douglas fir

Mt Thomas is a prominent foothill on the north edge of the Canterbury Plains north of the Ashley River. Native forests on the north and west sides are managed by the Department of Conservation while the exotic forest on the south and east aspects (including native forest pockets) is owned by Ngai Tahu Forest Estates and managed by the forestry company, Rayonier. Initially cleared for farming the farmed area was converted to plantations of Douglas fir (*Pseudotsuga menziesii*) and *Pinus* spp. after large scale erosion developed. Soils are derived from the shattered greywacke parent material either on bedrock or talus with some loess laid over the top in places.

The surveyed area is within the plantation and was chosen to get data from adjacent exotic and indigenous black beech forest and ranges from 430m up to 900m a.s.l. In practice the indigenous forest, already steep, was unsafe to traverse being dissected by ravines. Two short transects were achieved in the native forest, one following the main valley until blocked by a waterfall with plots at random distances off to either side, the other on a contour traverse across the heads of some ravines and below plantation forest which dominated the slope.

The exotic forest was mostly Douglas fir, a stand of *Pinus muricata* and on upper slopes another pine, possibly *P. nigra*. None of these had groundcover plants in their interiors, consequently short transects were used to sample from an edge into the forest until there had been at least one (occasionally two) plots in the zone devoid of groundcover.

Mt Grey

Mt Grey is a prominent foothill to the west of Amberley a little over 900m high. The study site is a native forest covenant at the southern end between 700 and 800m altitude. This forest is a mature remnant of black beech with some large red beech (*Fuscospora fusca*) and scattered Hall's totara (*Podocarpus cunninghamii*), there is a heavy groundcover of native ferns and moss and a good variety of smaller trees and shrubs appropriate to this altitude and wetter conditions. Geologically it is similar to Mt Thomas and they would at one time have had very similar vegetation.

Inland Sites

Melrose

Melrose is a sheep and beef station in the head of the Waipara catchment; it is farmed at a relatively low stocking and has plantation, forest remnants and large areas of grey scrub dominated by matagouri, *Discaria toumatou*. Rainfall is relatively light and the seasonal climate would be the most continental of all the sites studied. Transects were put into two main sites between 500 and 700m, one black beech forest remnant fenced to hold a number of deer and with very little groundcover, and the other a forested ravine that functions as a fence and trended east – west. For the latter the stream bed had to serve as the transect with plots being placed to alternate sides with a second transect on the north (south facing) slope above, which passed through grey-scrub and

collapsing black beech. A few additional but short transects were scattered in other pockets of woody vegetation.



Figure 3.4 Melrose plots from the southeast.

Glens of Tekoa

Glens of Tekoa is on the west side of the Mandamus River, a tributary of the Hurunui west of Culverden. On this farm there is an area of kanuka forest at around 400m a.s.l. which is grazed and an adjacent kanuka stand that had not been grazed for c.16yrs. Soils are derived from weathered greywacke alluvium and talus with a well-developed subsoil.

Island Hills

Island Hills is immediately north of Glens of Tekoa with similar climate and soils. Initially two main sites were considered a plantation of Douglas fir and a large beech forest covenant of roughly four square kilometres. After a day of exploration in the covenant no *D. filix-mas* had been found despite it being common in the adjacent

kanuka and grey-scrub on both sides of the Mandamus River. As a result transects were placed in the scrub and kanuka with transects ending in the beech forest. The Douglas fir stand was similar to Douglas fir on Mt Thomas in that the interior of the forest had no groundcover resulting in a similar approach being applied to that used on Mt Thomas.

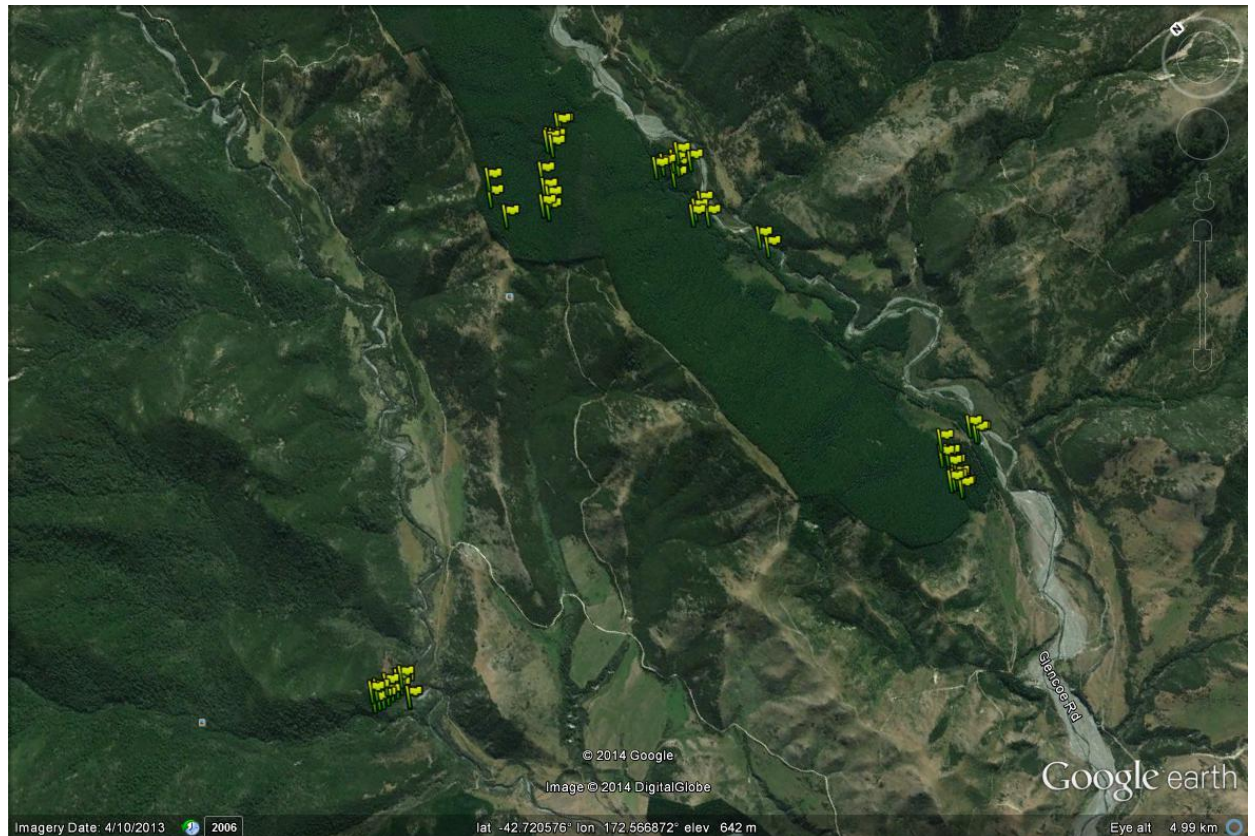


Figure 3.5 Island Hills plots, the cluster at bottom left go from beech forest through kanuka to frost-hollow grey scrub. Remaining groups are in Douglas fir.

3.3 Methods

3.3.1 Data collection

Data was collected over two periods: from mid-March 2011 to July 2011 and from December 2011 to end of March 2012. Survey for the foothills site, Mt Thomas, spanned both periods but in all other cases each site was surveyed in turn and completed before moving to the next site. Thus although data collection spanned two growing seasons, data at most sites was collected over no more than a few weeks.

Data was collected using a modification of the RECCE method for forest survey (Hurst and Allen 2007). For this survey, plot descriptors from the cover sheet and vegetation descriptors from the tier sheet were used. Modifications included: altering tier heights to suite the vegetation being surveyed; addition of a new category to 'Shape' – 'irregular'; using a spherical densiometer (Lemmon 1957) to measure the openness of the canopy and therefore the light potential. Canopy cover then became an estimate of large canopy gaps as there appeared to be a relationship between *D. filix-mas* abundance and canopy gaps in some situations. (Refer to appendix 6.1 for copies of both RECCE field sheets and the modified sheets used in this survey).

Standard RECCE scoring for plant species cover classes was used.

Unbounded plots of 5m radius were located at 50 metre spacings on parallel transects 50 metres apart within a forest remnant, with the transect bearing chosen to cross landscape features and sample all landforms present. The first transect origin was chosen prior to arriving at the survey site by marking the transect on an aerial photograph and then locating the indicated origin in the field. The first plot was then spaced at a random distance in from the edge. Each plot was centred on the transect with boundaries adjusted to exclude adjacent landforms to avoid recording plants from highly contrasting sites, to obtain more accurate floristic and geographic descriptions. At Tiromoana Bush the plot centre was also indicated with a 'Permolat' marker attached to the nearest tree.

Aspect was measured to the nearest degree using a hand held compass and slope was measured using a handheld inclinometer with both being taken across the centre of the plot.

The densiometer was used in each plot to estimate canopy density, which in turn is a proxy for the light permeability of the canopy over and around the plot. As most canopies were dense this tool was used to estimate the amount of sky overhead. 0 would be no sky visible and 96 (the highest value) an unobstructed sky. Four estimates were taken around the centre of the plot facing each of the cardinal points at a height of around 1m as the species of interest (*D. filix-mas*) seldom exceeds 1m and in some of the seral communities a dense shrub layer was present between 1.2 and 1.7m.

Landform describes the physical feature of the landscape: Gully (G), Terrace (T), Face(F) and Ridge (R). It is then further described with the Shape category: Concave, Convex, Linear and I added a fourth “Irregular” to describe sites affected by tunnel gully erosion, slumping and landslide deposits which are common features in landscapes with deep loess deposits but do not comfortably fit with the conventional landform descriptors, and because *D. filix-mas* and other ferns are likely to be affected by changes at the micro-site scale of the landscape.

Groundcover classes were also estimated using the accepted classes of Rock, Bare ground, Litter, Bryophytes and Vascular as a percentage of cover with all classes together summing to 100%. An observed increase in one class will have a negative reciprocal in one or more of the remaining classes.

Vegetation was recorded and estimated following the RECCE convention except that tier heights were lowered to separate the shrub and understory at the maximum height for *D. filix-mas* of 1m. This resulted in groundcover (<30cm), shrublayer (30cm – 1m), understory (1m – 5m), Canopy (>5m). There were very few instances where understory plants exceeded 5m. Cover classes were scored according to convention i.e.

‘1’ < 1%, ‘2’ 1 – 5%, ‘3’ 6 – 25%, ‘4’ 26 – 50%, ‘5’ 51 – 75%, ‘6’ > 75%.

3.3.2 Data entry and calculations

Importance values (IV) were calculated for each species in each tier and then summed to give an overall IV for each species using the formula in Norton and Leithwick (1990):

$$IV = \sum_i^n (\log_{10} \text{median tier height}) * \text{species cover score}$$

The Compass bearings for aspect were adjusted to approximate True North by adding 23° (declination over North Canterbury is between 22.8 and 23.5°) and then, because the ordination software cannot work with non-continuous values, bearings were further adjusted for ordination by subtracting values from 181° – 359° from 360° to get values from 1° to 179°. This gives a situation where north and south are the most dissimilar, while east and west are equal at 90°.

Densiometer readings were averaged to give a single value for each plot but were not further transformed, therefore the value is out of 96.

3.3.3 Ordination and analysis

The program 'CANOCO for Windows 4.54' was used to conduct detrended correspondence analysis (DCA) to identify floristic patterns and the potential drivers of those patterns. While DCA has many detractors (Legendre and Legendre 1998, McCune and Grace 2002) all ordination methods have their weaknesses and DCA is an effective method for this study.

In the ordination approach used here (DCA) each species is first placed in a multi-dimensional space according to its relationship to all other species. Sample points (plots) are then fitted according to the floristic pattern; environmental attributes are similarly related to the floristic pattern and assigned values and directions which can be interpreted as influence on species distributions. The biggest problem with ordination comes with interpreting the results when many axes are projected into just two axes. In representing this multi-dimensional data in a two dimensional scatterplot it can be assumed that most species clustered near the edges are close to each other in ordinated and real space, that samples can be viewed similarly and that species that occur near samples are generally associated with those samples. This does not hold true however for the centre of the graph where we are looking through the ordinated space from one side to the other. Because rare species are likely to be positioned at the peripheries due to a lack of meaningful data, the most meaningful points are probably those that lie midway between the centre and edges of the plot (Jongman et al. 1995). CANOCO arranges species such that the first and second ordination axes contain most of the explainable variation in the species data. Further comparisons can be made with the third and fourth axes if required.

Ordinations were conducted using default settings with a few minor changes being made. *D. filix-mas* was made supplementary so as not to influence the ordination; where the canopy was primarily one species it was down-weighted to 0.2 (from 1) e.g. kanuka, *Kunzea ericoides*, at Tiromoana Bush; and rare species were down-weighted. Any deviations from this are noted in the results section for the particular ordinations.

Data from each tier and all tiers combined was ordinated and the resulting solution files used to create graphs in R with those plots containing *D. filix-mas* differentiated. Ordinations that effectively grouped *D. filix-mas* were further analysed using ANOVA and the ordination axes in the R statistical package.

The main environmental variables were analysed in R using generalised linear models (GLM) of the poisson and binomial families. Where over dispersion was evident, data was further analysed with quasipoisson and quasibinomial as appropriate.

3.4 Results

3.4.1 Tiromoana Bush

Ordinations with DCA

Ordinations with all tiers were carried out and the solution files used to graphically represent the distribution of male fern in the ordinated plots. Separate ordinations with species data for canopy, with understorey and with shrublayer did not show any clear separation of plots that contain *D. filix-mas*. Consequently only the ordinations from the combined dataset and the groundcover dataset are described and further analysed.

Combined dataset (all tiers)

This dataset has 78 samples and 138 species

The ordination with all vegetation tiers provides an overview of species – species relationships and species – environment relationships at Tiromoana Bush but clear groupings were not evident with some anomalous species placements. However there are strong positive correlations on Axis1 relative to light and vegetative groundcover and strong negative correlations to aspect and slope, with a moderate negative correlation with canopy height (Figure 3.6). The first axis explains 12% of the variance in the species data and 22% of the species – environment correlation, while for the second axis this is 10% and 6% respectively (Table 3.1).

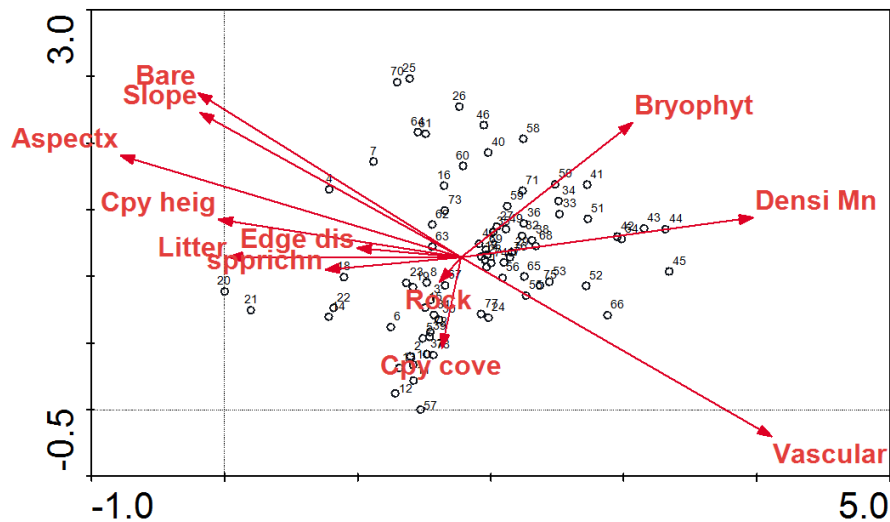


Figure 3.6 Tiromoana Bush DCA ordination plot and environmental factor relationships derived from species data for all tiers. Figure generated in Canoco Draw, note that Canoco limits names to 8 characters. Aspectx is aspect converted to degrees from North, therefore both East and West are 90°. Densi Mn (densiometer mean) is a proxy for light being a measure of how open the canopy is. Cpy cove (canopy cover) in this instance is a measure of gaps between canopy trees.

When looking at the plot distribution (Figure 3.6) the only clear pattern is that most plots from plot 32 – 46 are to the right of the centroid for the environmental factors.

The majority of these plots are from a north-facing area where groundcover is dominated by the turf forming native grass *Microlaena stipoides* growing under a relatively thin and low kanuka canopy with very few shrubs. This is consistent with the interpretation of the environmental gradients mentioned above.

The species ordination (Figure 3.7) has two reasonably clear groupings: the top right quarter with a mix of native and exotic plants characteristic of hot, dry and exposed conditions and below this is a further small group of exotic grasses and herbs tolerant of dry conditions but more generalist than the second group. A third group in the top left quarter of the plot contains plants that are nearly all native and characteristic of average forest conditions as well as plants of wet forest conditions. The dominant canopy species, kanuka, occurs near the centre, and the remaining plants scattered around the centre and into the lower left quarter are either rare in the data or are generalists.

Overall the dominant pattern from the species – environment ordination places warm, dry plants to the right and cool (shaded) and moist plants to the left. Most of the plants characteristics of wet and heavy soils are found in the upper middle of the plot, forming

a subgroup of the third group. *D. filix-mas* is positioned among exotic and native generalist species, and while some species that it appears to commonly associate with are nearby such as *Cerastium fontanum* and *Myelis muralis* others such as *Polystichum richardii*, *Dactylus glomeratus* and *Coprosma rhamnoides* are widely scattered by the ordination.

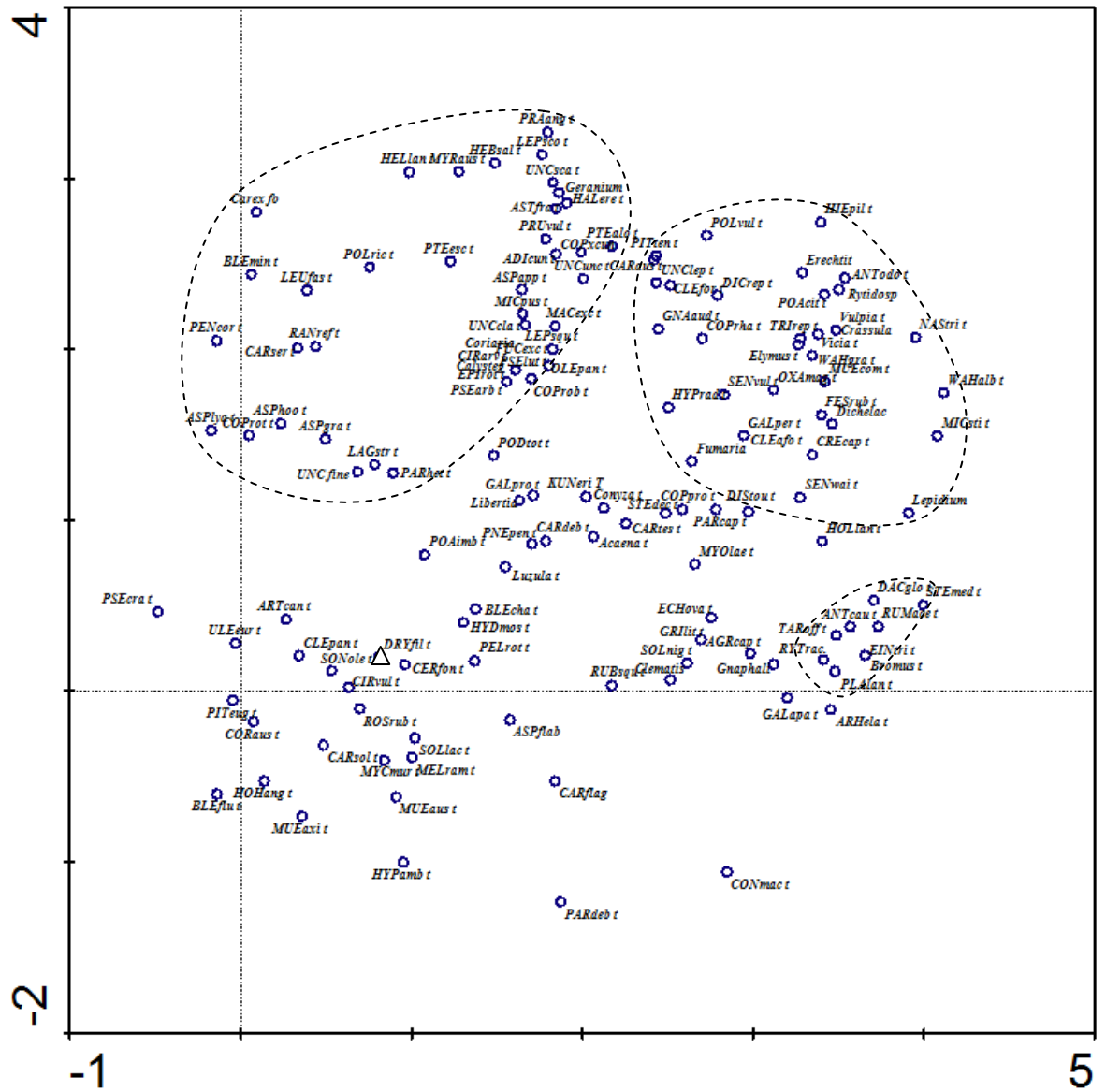


Figure 3.7 Species relationships from Axes 1 and 2 of the DCA for all tiers at Tiromoana Bush. *D. filix-mas* Δ is in the bottom left quarter. Dryland plants and high light are on the right.

Table 3.1 Summary statistics for the Tiromoana Bush DCA ordination axes

| | Eigenvalue | Gradient length | Species – environment correlation | % variance explained | |
|----------------------------------|------------|-----------------|-----------------------------------|----------------------|-----------------------|
| | | | | species | Species - environment |
| DCA with all forest tiers | | | | | |
| Axis 1 | 0.48 | 3.34 | 0.68 | 12 | 22 |
| Axis 2 | 0.37 | 2.49 | 0.45 | 10 | 6 |
| Axis 3 | 0.29 | 2.97 | 0.64 | 6 | - |
| Axis 4 | 0.16 | 2.27 | 0.60 | 15 | - |
| DCA with groundcover tier | | | | | |
| Axis 1 | 0.73 | 4.25 | 0.87 | 10 | 25.5 |
| Axis 2 | 0.46 | 3.66 | 0.57 | 6 | 6 |
| Axis 3 | 0.38 | 3.29 | 0.70 | 6 | - |
| Axis 4 | 0.26 | 3.19 | 0.62 | 4 | - |

Groundcover dataset

The groundcover ordination considered 78 samples and slightly fewer species, 131, than the combined ordination at 138. Using only the species and values present in the groundcover layer this ordination has quite a different appearance to the species graph for all species (arrow shaped rather than round) but on closer inspection it is surprisingly similar and makes more sense.

Axis 1 has a gradient length > 4 which implies a unimodal response to species data (Ter Braak and Smilauer 2002) explaining 10% of the variance in the species data and 26% of the species – environment correlation. While for the second axis this is 6% and 6% respectively (Table 3.1). The other axes show a moderate correlation to species.

The environmental factors are represented in Figure 3.8. Aspect, canopy height and slope continue to have a strong negative relationship to axis 1 and are joined in this regard by species richness. Light permeability (Densi.Mn) continues to have a strong positive relationship with axis 1 but also has a strong negative relationship with axis 2. Edge distance has a moderately negative relationship to both axes.

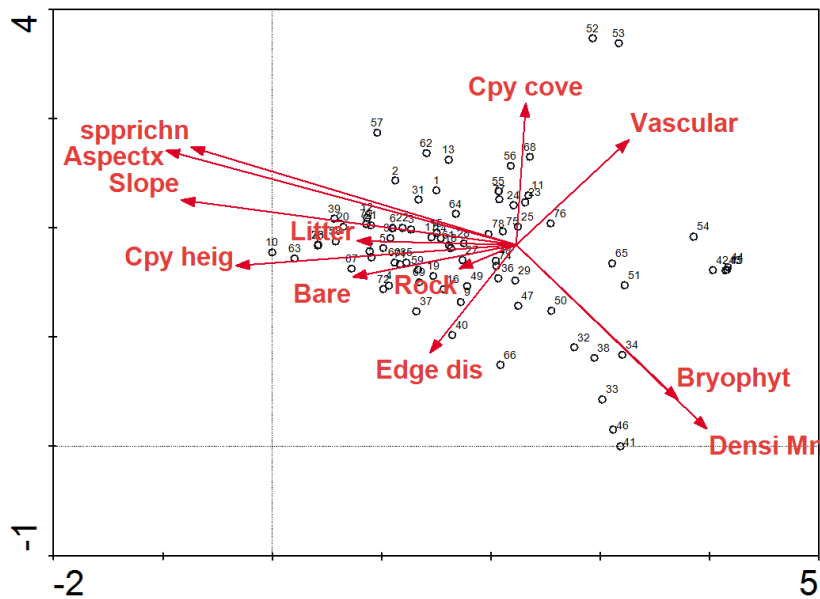


Figure 3.8 Samples and environment plot for Tiromoana Bush groundcover tier.

On the species plot (Figure 3.9), species appear to be largely arranged on two diagonal axes, these fit best with a light gradient going from low light in the top left corner to high light, hot and dry in the bottom right corner. The second diagonal axis starts near the top right corner with species that have high light requirements but at Tiromoana, were often in areas with low overhead light and strong peripheral light from a nearby edge or gap such as *Anthriscus caucalis* and *Parsonsia capsularis* seedlings. This axis then descends toward the bottom left corner and loses definition toward the centre of the plot. As with the combined ordination, plants associated with dry sites are mostly to the right of axis 1 but there is no clear distinction between plants commonly associated with wet sites and the remaining species. From this ordination two groups of plants can be clearly discerned, one representing species found in shaded but high light areas (top right) and the other representing high light, hot and dry conditions. *D. filix-mas* is positioned at centre-left of the plot and again, the remaining plants are more generalist or suited to moist soil sites but are not clearly separated.

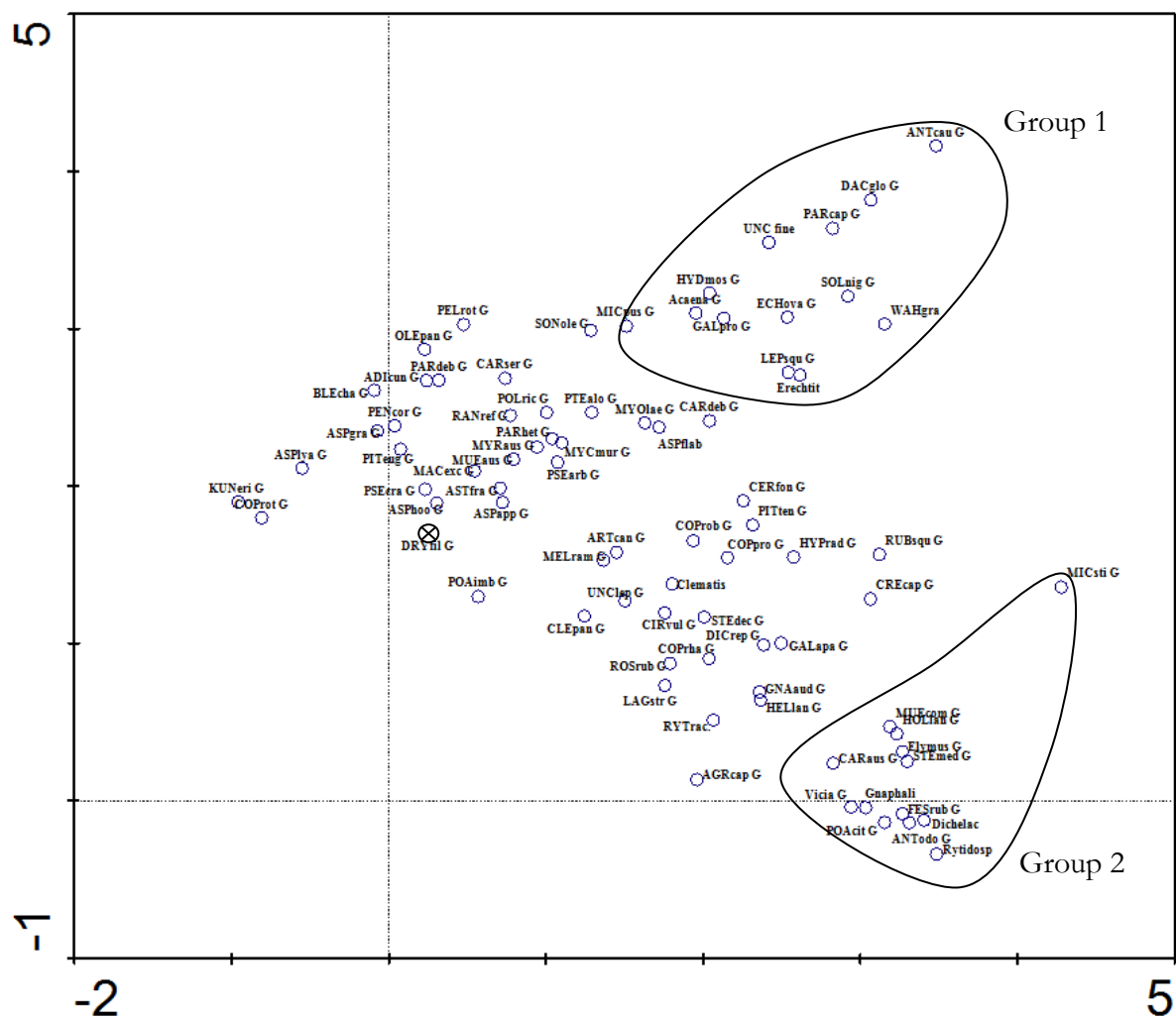


Figure 3.9 Tiromoana Bush DCA plot for groundcover species with rare species (less than 4 records) not shown for clarity. Group 1: cool with overhead shade but plentiful peripheral light from the forest edge. Group 2: high light, hot and dry. *D. filix-mas*, marked with ⊗.

Statistical analyses

Anova with ordination axes and *D. filix-mas* presence

One-way Anova for male fern presence was statistically significant for axis 1 of the ordination for groundcover ($P = 0.0018$). No significance was found with the other axes in the groundcover ordination or any axes in either the ordination for all tiers or an ordination using environmental attributes only. While Anovas for *D. filix-mas* against the second and third ordination axes of the groundcover dataset was not statistically significant, when graphed in a scatterplot (Figure 3.10) axis 2 as well as axis 1 demonstrate a clear subset of plots for *D. filix-mas* presence. Anova outputs are summarised in Table 3.2.

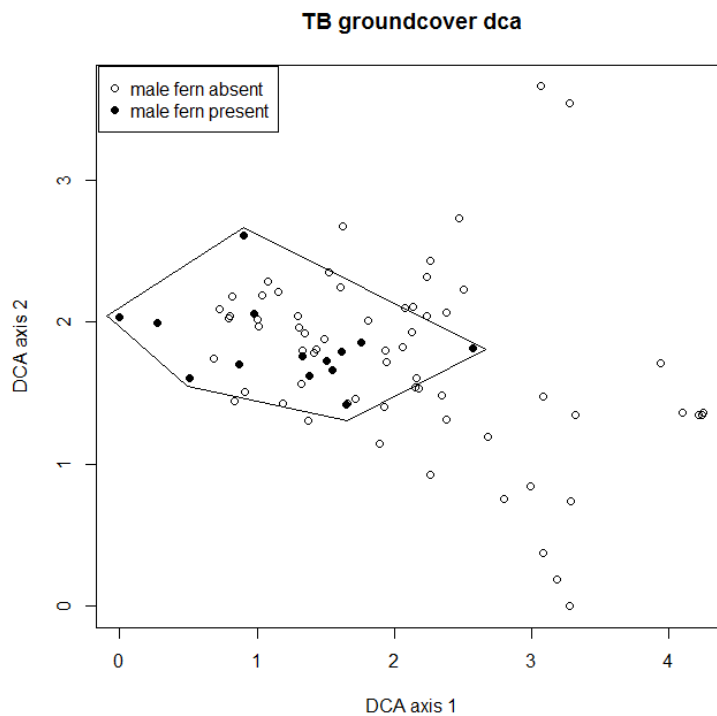


Figure 3.10 Distribution of plots with *D. filix-mas* at Tiromoana Bush within the ordinated space defined by axes 1 and 2 of the groundcover DCA. F-value 10.42, $P < 0.0018$

Table 3.2 Summary of one way Anova output for *D. filix-mas* presence against DCA ordination axes. (Degrees of freedom = 1 with 76 residuals in each instance).

| Tiromoana Bush | Sum of Squares | Mean of Squares | F value | Significance P |
|-----------------------------------|----------------|-----------------|---------|----------------|
| DCA for environments only | | | | |
| Axis 1 | 0.280 | 0.27992 | 3.007 | 0.087 |
| Axis 2 | 0.065 | 0.06479 | 1.112 | 0.295 |
| Axis 3 | 0.0478 | 0.04785 | 1.277 | 0.262 |
| DCA for all tiers combined | | | | |
| Axis 1 | 1.097 | 1.0971 | 2.795 | 0.0987. |
| Axis 2 | 254 | 0.2539 | 0.881 | 0.351 |
| Axis 3 | 0.005 | 0.00495 | 0.026 | 0.872 |
| DCA for groundcover only | | | | |
| Axis 1 | 8.68 | 8.681 | 10.42 | 0.0018 ** |
| Axis 2 | 0.115 | 0.1146 | 0.324 | 0.571 |
| Axis 3 | 0.3 | 0.3042 | 0.529 | 0.469 |

Anova for environmental factors with *D. filix-mas* presence

In the ordinations, slope, aspect, light and species richness had the strongest correlations with species distributions. Only aspect has a statistically significant relationship with the distribution of *D. filix-mas* ($P=0.0067$). Significance of environmental factors is summarised in Table 3.3 and the distribution of *D. filix-mas* for slope (no relationship) against aspect ($0 - 180^\circ$) is shown in Figure 3.11.

Table 3.3 Significance of environmental factors for *D. filix-mas* presence/absence from Anova

| Densimeter | Edge | Slope | Canopy | Species | Aspect | Canopy |
|------------|----------|-------|--------|----------|-------------------|--------|
| Light | distance | | Cover | Richness | ($0-180^\circ$) | Height |
| 0.486 | 0.267 | 0.781 | 0.77 | 0.392 | 0.0067 ** | 0.514 |

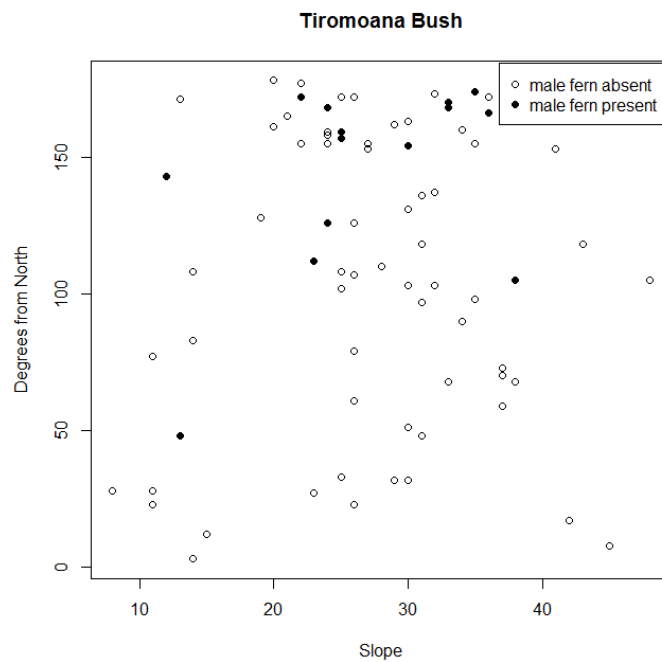


Figure 3.11 Slope has no influence on *D. filix-mas* but most *D. filix-mas* are found on aspects to the South of East and West (>90 on y axis), $P=0.0067$.

Categorical environment factors

Graphs produced in Excel suggest patterns for *D. filix-mas* distribution against the categorical factors Landform, Shape and Aspect (expressed as N, NE, E, etc)(Figure 3.12, Figure 3.13). Analysis with generalised linear models confirms that even with the large variance in the data each of these categories is significant for the distributions of *D. filix-mas* at Tiromoana Bush.

Table 3.4 Significance values for the categorical explanatory variables at Tiromoana Bush

| | Aspect | Landform | Shape |
|---------|--------|----------|---------|
| P value | 0.0002 | 0.0435 | <0.0001 |

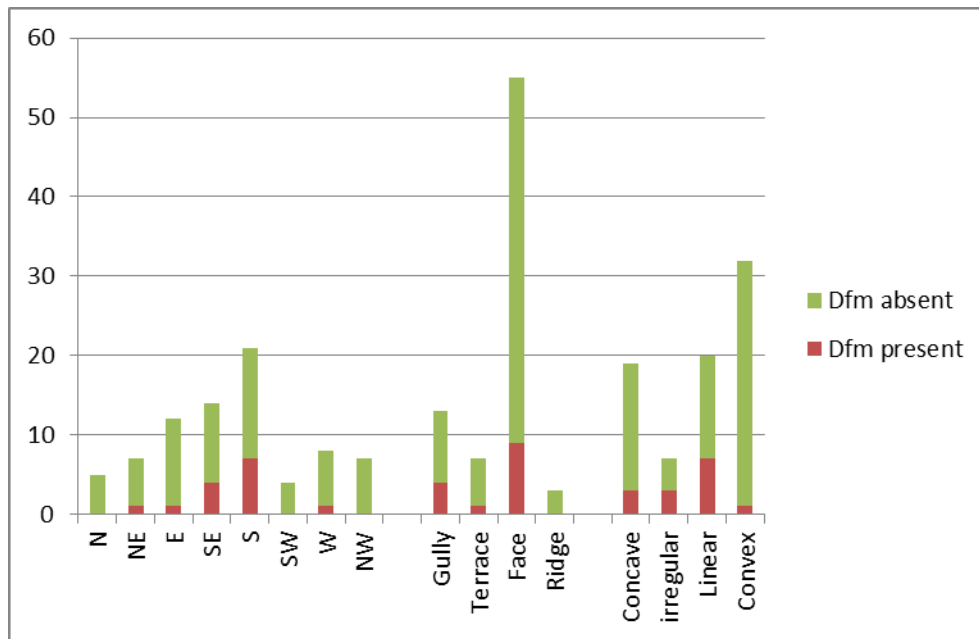


Figure 3.12 Number of plots in each categorical environment category with the total number of plots with male fern at right (presence).

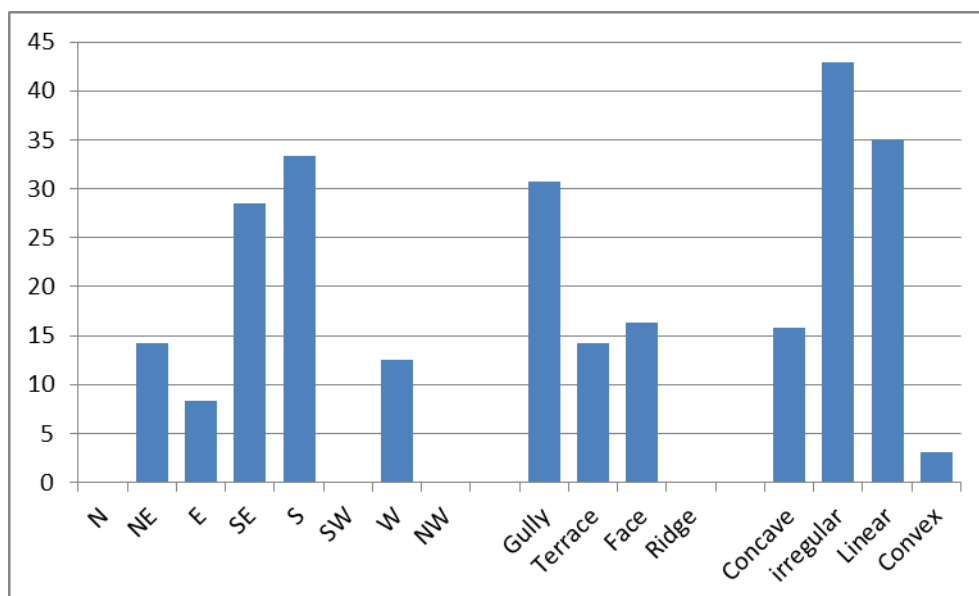


Figure 3.13 *D. filix-mas* occurrence expressed as the percentage of plots in each category that contain *D. filix-mas*.

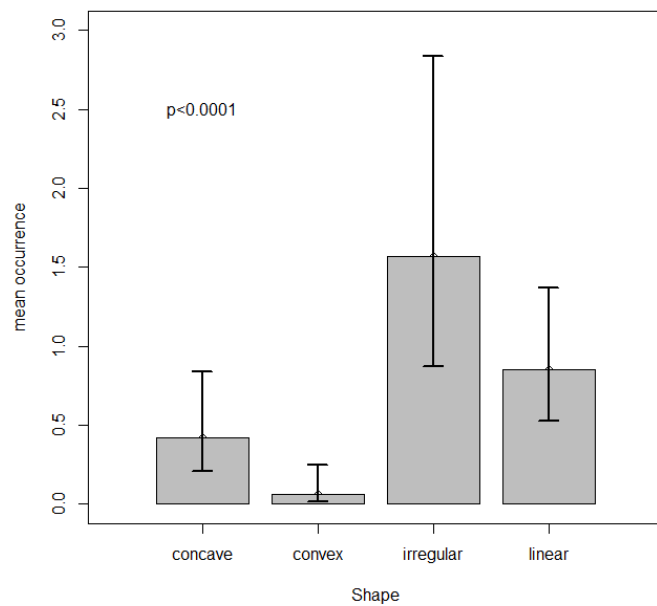


Figure 3.14 Mean number of *D. filix-mas* in plots of different surface shapes, standard error bars are 95% CI, $P < 0.0001$. Irregular surfaces are the uneven surfaces resulting from tunnel-gully erosion, slumping and landslides.

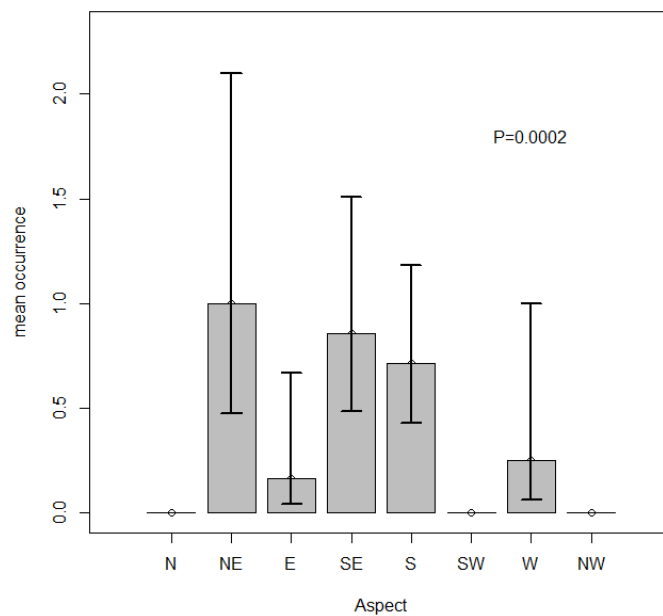


Figure 3.15 Mean number of *D. filix-mas* in plots of different aspect, standard error bars are 95% CI, $P = 0.0002$

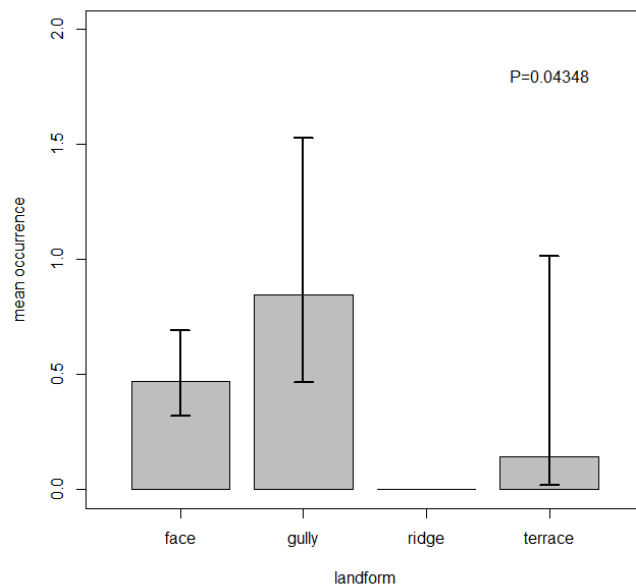


Figure 3.16 Mean occurrence of *D. filix-mas* on different landforms, standard error bars are 95% CI, $P = 0.0435$.

3.4.2 North Canterbury foothills and inland sites

Ordination with DCA

The combined dataset (all tiers)

This dataset has 257 active samples and 253 active species.

Axis 1 is moderately correlated with environmental data (0.638), explaining 5% of the species variance and 19% of the species – environment relationship. The other axes are only weakly correlated and summary statistics are presented in Table 3.5.

Light permeability and species richness have a strong negative relationship to axis 1 while canopy height has a strong positive relationship. Both altitude and canopy intactness have a moderate positive relationship on axis 1.

Anova suggests that axis 1 is also significant for the presence of *D. filix-mas* ($P < 0.0001$). However axes 2, 3 and 4 are not.

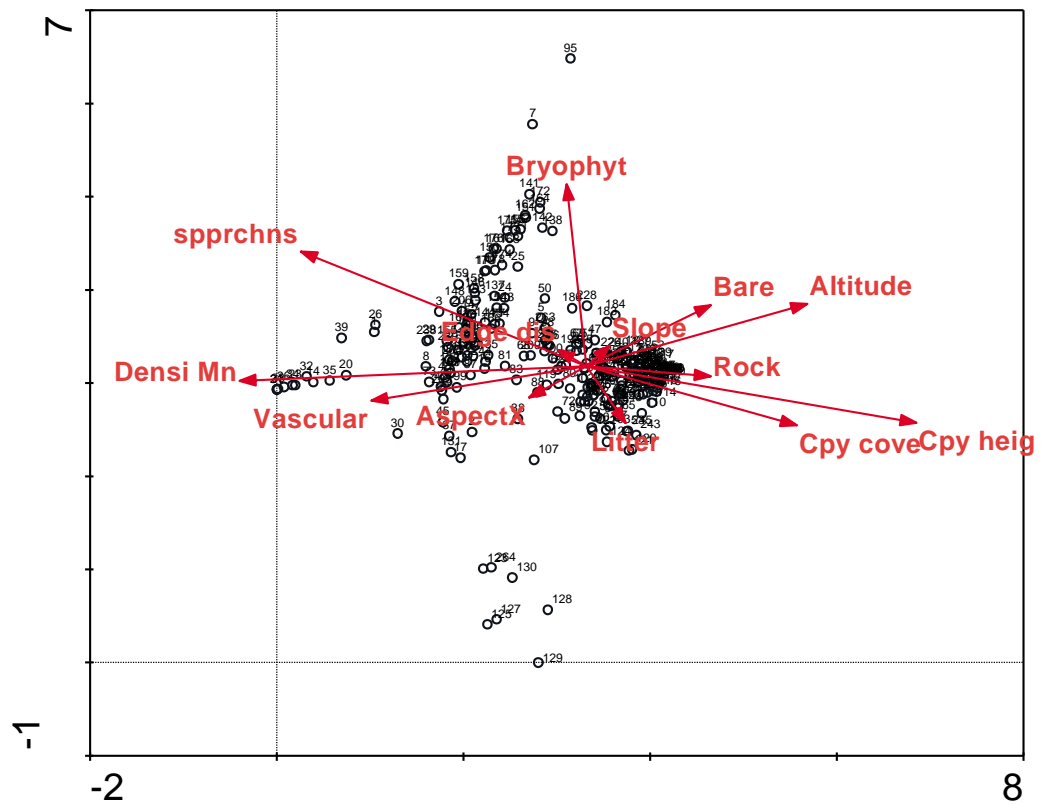


Figure 3.17 Sample and environment plot for the DCA ordination of all tiers with the foothills and inland sites datasets. A possible arch effect on axis 2 is evident.

No floristic pattern could be discerned with this overall ordination and there is a possible arch effect with samples on axis 2 (Figure 3.17) which looks like it may be repeated in the species ordination(Figure 3.18).

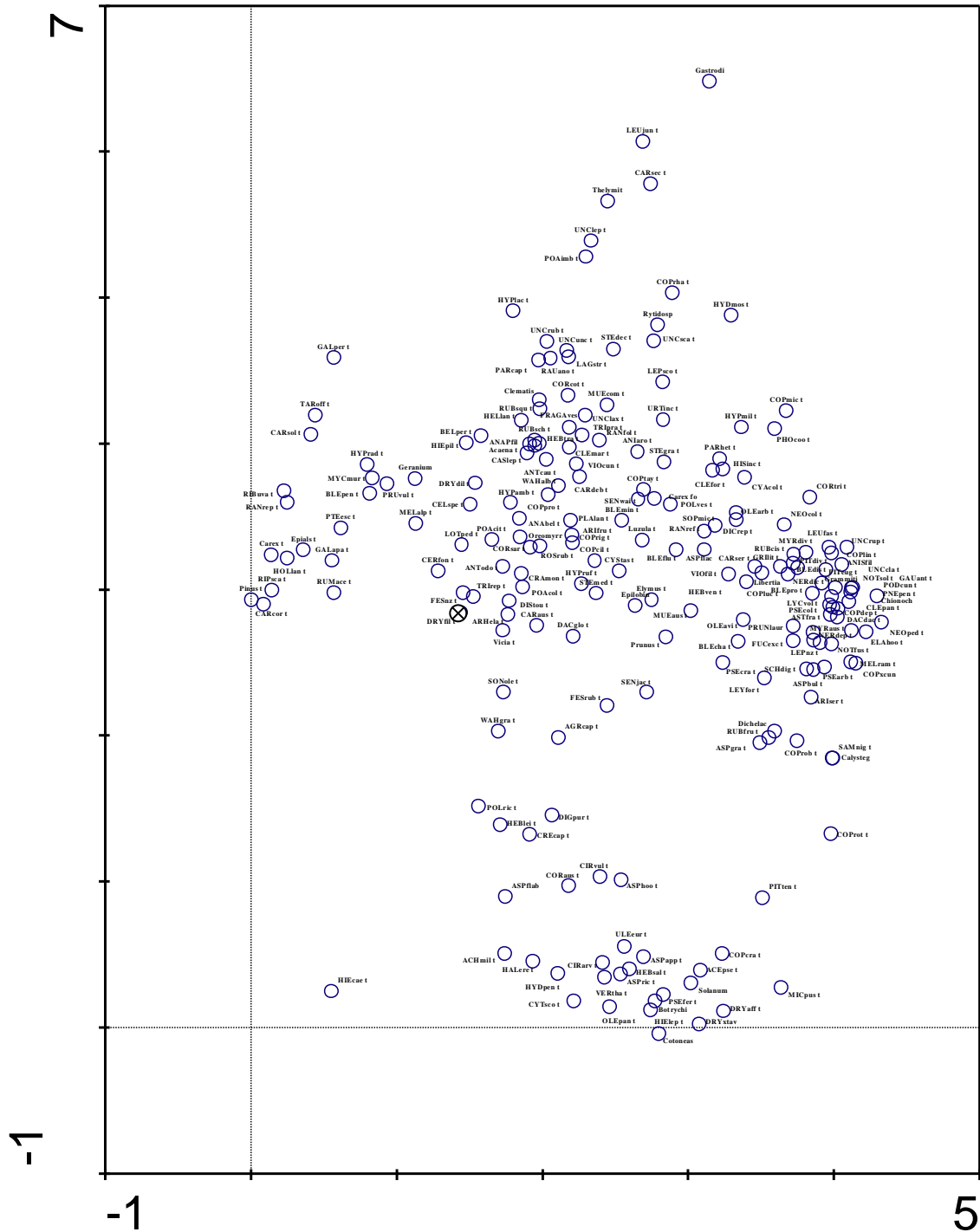


Figure 3.18 Species plot for the DCA ordination of all tiers, with foothills and inland sites dataset. *D. filix-mas* is marked ⊗

Table 3.5 Summary statistics for foothills and inland sites DCA ordination axes

| | Eigenvalue | Gradient length | Species – environment correlation | % variance explained species | Species - environment |
|----------------------------------|------------|-----------------|-----------------------------------|------------------------------|-----------------------|
| DCA with all forest tiers | | | | | |
| Axis 1 | 0.86 | 4.12 | 0.64 | 5.4 | 18.8 |
| Axis 2 | 0.67 | 6.48 | 0.41 | 4.2 | 3.9 |
| Axis 3 | 0.50 | 5.29 | 0.33 | 3.2 | - |
| Axis 4 | 0.40 | 4.15 | 0.34 | 2.5 | - |
| DCA with groundcover tier | | | | | |
| Axis 1 | 0.78 | 6.08 | 0.77 | 5.4 | 25.9 |
| Axis 2 | 0.48 | 7.29 | 0.48 | 3.4 | 7.1 |
| Axis 3 | 0.41 | 3.64 | 0.56 | 2.9 | - |
| Axis 4 | 0.33 | 3.67 | 0.45 | 2.3 | - |

Ordination with DCA for the groundcover dataset

The groundcover ordination considered 248 samples and 235 species, summary statistics are presented in Table 3.5 above.

Axis 1 is highly correlated with the environmental data explaining 5% of the species variance and 26% of the species – environment relationship. The remaining axes are only weakly to moderately correlated with the environmental data although axis 2 does explain a further 7% of the species – environment relationship.

Plots and environmental attributes are graphed on axes 1 and 2 (Figure 3.19), showing that light permeability has a strong negative relationship to axis 1, while canopy height and canopy intactness have strong positive relationships. Altitude has a moderate positive relationship to both axes, species richness has a moderate negative relationship to axis 1 (increasing with light), while aspect has almost no relationship at all.

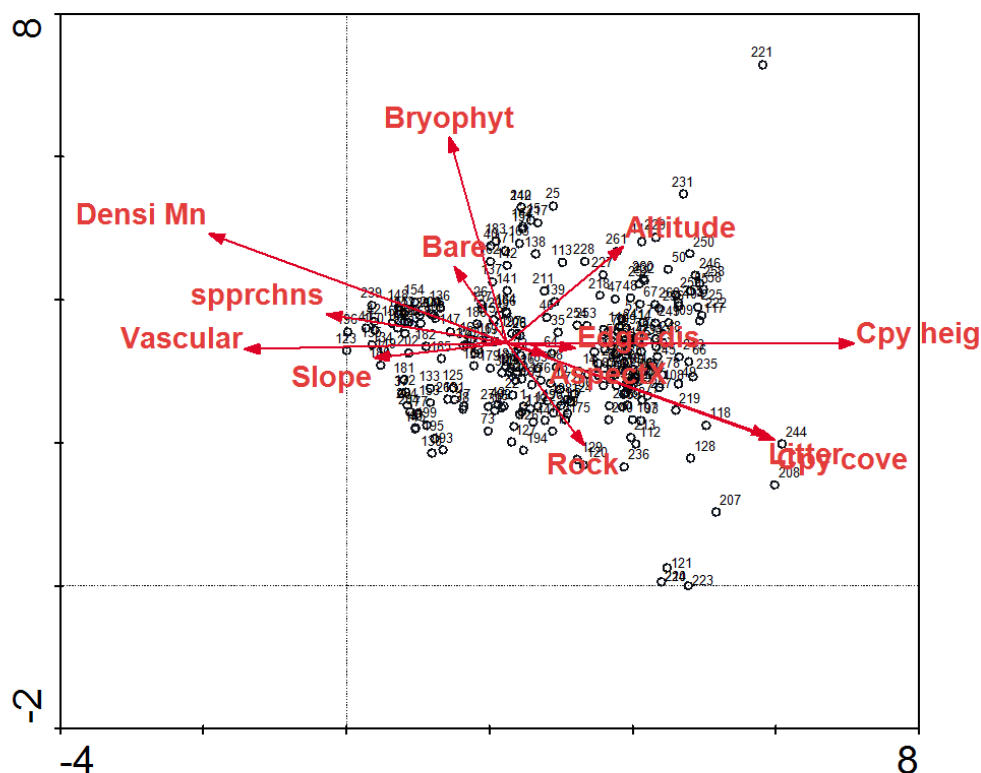


Figure 3.19 Sample and environment gradient plot from groundcover DCA with the foothills and inland dataset

Anova with ordination axes

All four principal axes from the ordination of the groundcover data are significant for the presence of *D. filix-mas* which is presented in the table below and presented in graphically in Figure 3.21 and Figure 3.22.

Table 3.6 Results from Anova for the axes of the foothills and inland sites groundcover DCA ordination. P is significant at: *** 0.001, ** 0.01, * 0.05.

| | Df | Sum Sq | Mean Sq | F value | P |
|--------|----|--------|---------|---------|--------------|
| Axis 1 | 1 | 36.00 | 36.030 | 21.93 | 4.67e-06 *** |
| Axis 2 | 1 | 16.77 | 16.774 | 21.39 | 6.07e-06 *** |
| Axis 3 | 1 | 4.90 | 4.901 | 11.30 | 9e-04 *** |
| Axis 4 | 1 | 2.01 | 2.0079 | 5.20 | 0.0235 * |

In the species ordination plot, Figure 3.20, some rough groups emerged with a predominance of grey-scrub/grassland species to the left (high light environment); montane and inland species to the upper right and in the lower right a small cluster of species characteristic of damp and shady sites in the areas surveyed such as gullies. Exotic species increase to the bottom and left of the ordination plot where *D. filix-mas* is

found at the lower edge and left of centre. Consequently *D. filix-mas* is most strongly associated with exotic species.

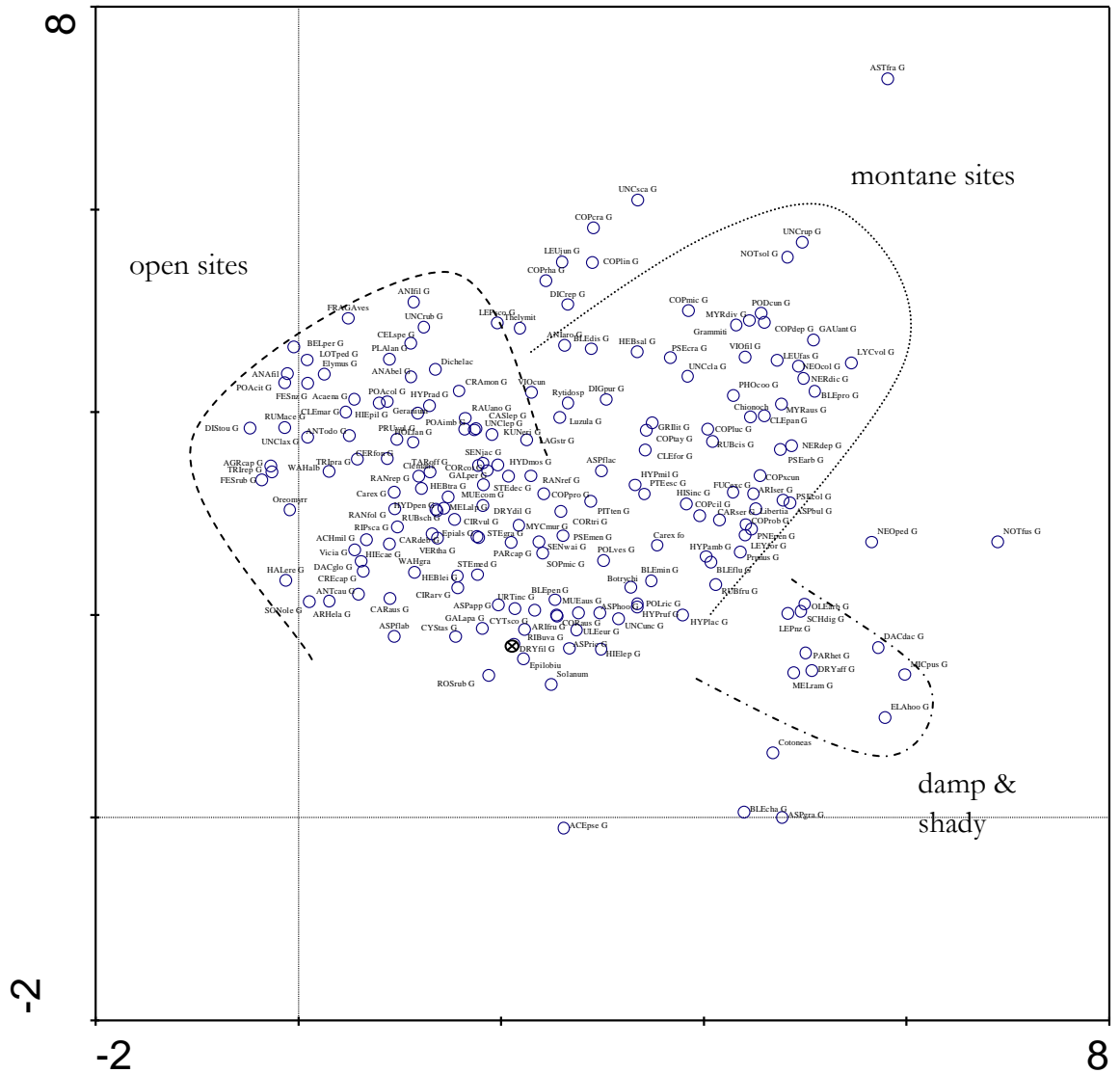


Figure 3.20 Groundcover species DCA ordination for North Canterbury foothills and inland sites. Species with only one occurrence are not shown for simplicity. *D. filix-mas* is marked ⊗. In the upper left, species are characteristic of open sites and grey scrub, higher altitude and unmodified forest in the upper right, with *D. filix-mas* in the lower middle associated mostly with exotic species indicative of disturbance.

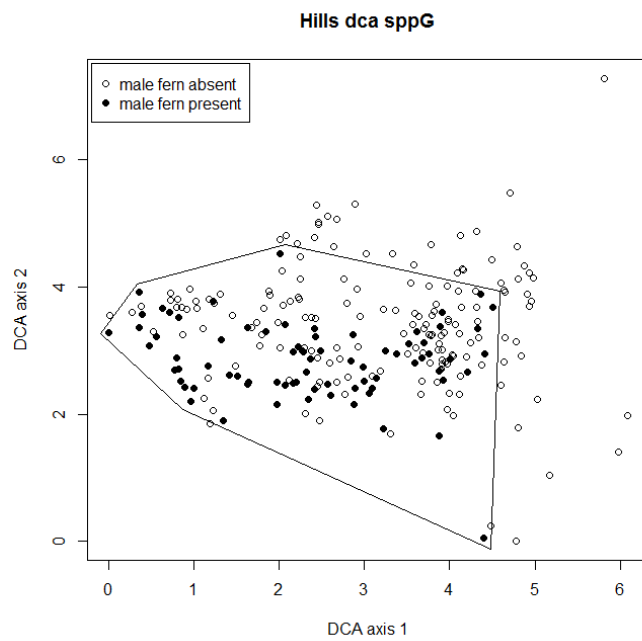


Figure 3.21 Axes 1 and 2 from the foothills and inland site groundcover ordination showing the distribution of plots with and without *D. filix-mas*.

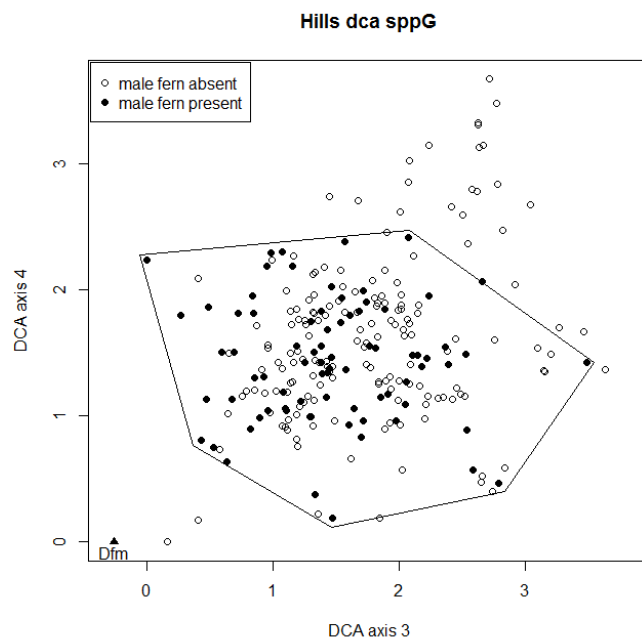


Figure 3.22 Axes 3 and 4 from the foothills and inland site groundcover ordination showing the distribution of plots with and without *D. filix-mas*.

Results for environmental factors

Analysis of the full dataset using GLM to compare *D. filix-mas* with the environment attributes suggest that only species richness, altitude and land shape are significant predictors for *D. filix-mas*. However, when plots from the main sites (Mt Thomas, Mt Grey, Melrose, Glens of Tekoa and Island Hills) were divided into plantation and non-plantation and analysed separately, light permeability (densiometer) came out as significant for non-plantation plots (Figure 3.24 and Figure 3.25) and aspect (0° - 180°) as significant for plantation plots. Significance values for all analyses are summarised in Table 3.7.

Table 3.7 Significance (P values) of the presence of *D. filix-mas* for the continuous variables in the foothills and inland sites dataset from GLM. Significance level codes: * 0.001; ** 0.01; * 0.05**

| | Plantation | Non-plantation | All plots combined |
|--------------------------------------|------------|----------------|--------------------|
| Densiometer/Light | 0.2479 | 0.0275* | 0.5677 |
| Slope | 0.0675 | 0.7859 | 0.2448 |
| Canopy intactness | 0.6694 | 0.2480 | 0.4540 |
| Species richness | 0.1275 | 0.0004** | 0.0069** |
| Aspect ($0-180^{\circ}-0^{\circ}$) | 0.0085** | 0.2663 | 0.5612 |
| Canopy height | 0.4952 | 0.1473 | 0.7242 |
| Altitude | 0.4289 | 0.0249* | 0.0103* |
| Aspect (N, NE, E...) | 0.9637 | 0.3082 | 0.9283 |
| Landform | 0.6842 | 0.2832 | 0.2097 |
| Land shape | 0.0314* | 0.3072 | 0.0364* |

Sites with higher diversity (species richness) are slightly (c. 16%) more likely to contain *D. filix-mas*, $P=0.0069$ overall and this effect is slightly stronger when plantation sites are excluded (Figure 3.23).

Aspect had a significant response in plantation plots in the form used for ordination where aspects greater than 180 were reduced to their equivalent value on an east aspect, e.g. 181 becomes 179 and 270 (west) becomes 90. This is presented in Figure 3.26

below, where it can be seen that most plots with *D. filix-mas* and those with the higher counts fall between 75 and 180 corresponding to plots trending south rather than north.

Altitude was significant in the analysis of both the full dataset and the non-plantation plots with a reduction in occurrence above 600m a.s.l. and is presented in Figure 3.27 and Figure 3.28.

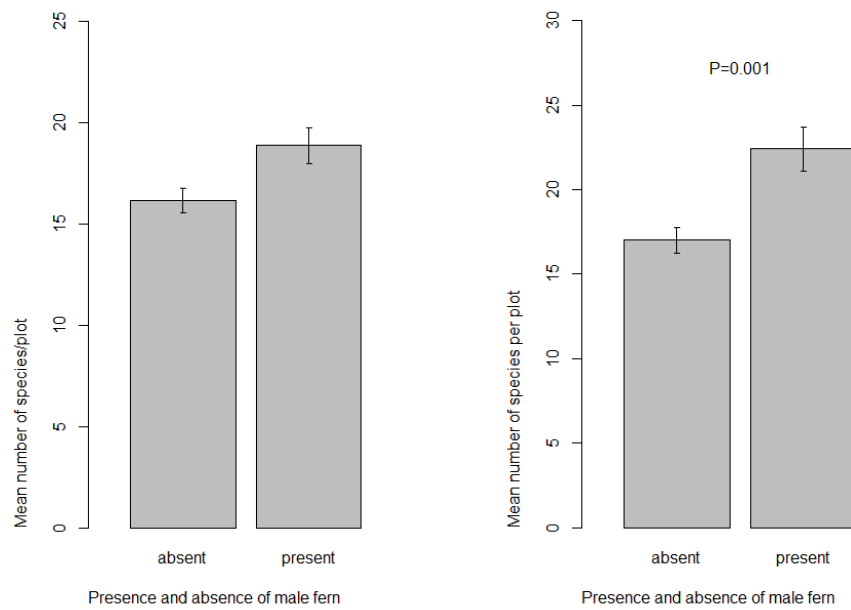


Figure 3.23 Plots with and without *D. filix-mas* against species richness. On the left for all foothills and inland plots (P=0.0069) and on the right for non – plantation sites (P=0.001).

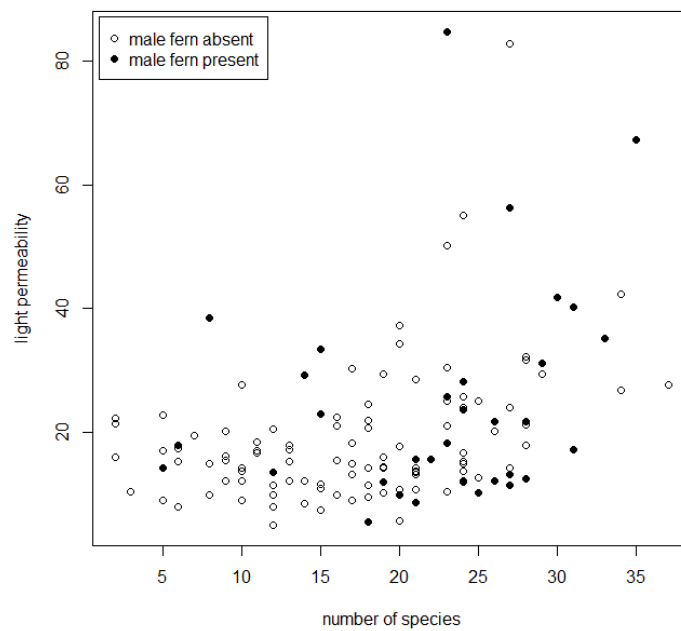


Figure 3.24 Species diversity compared to light permeability with the non-plantation data. This plot is primarily to better illustrate the relationship of *D. filix-mas* to light permeability (Figure 3.25) and species diversity (Figure 3.23). *D. filix-mas* is rare with light permeability <7% and conditions that favour species diversity also favour *D. filix-mas* (most *D. filix-mas* are in sites with more than 20 species).

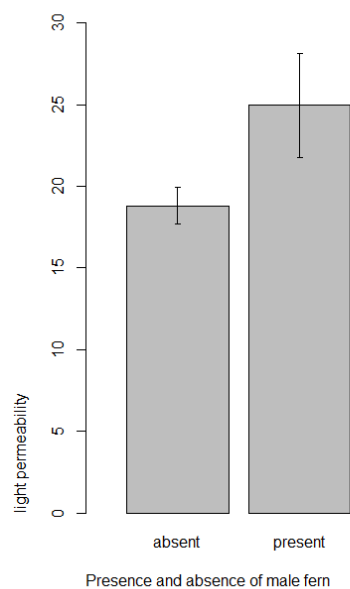


Figure 3.25 Non-plantation, canopy light permeability for *D. filix-mas* presence, $P = 0.0275$ with mean and standard error of: absent - 18.8 and 1.1, and present 24.9 and 3.2.

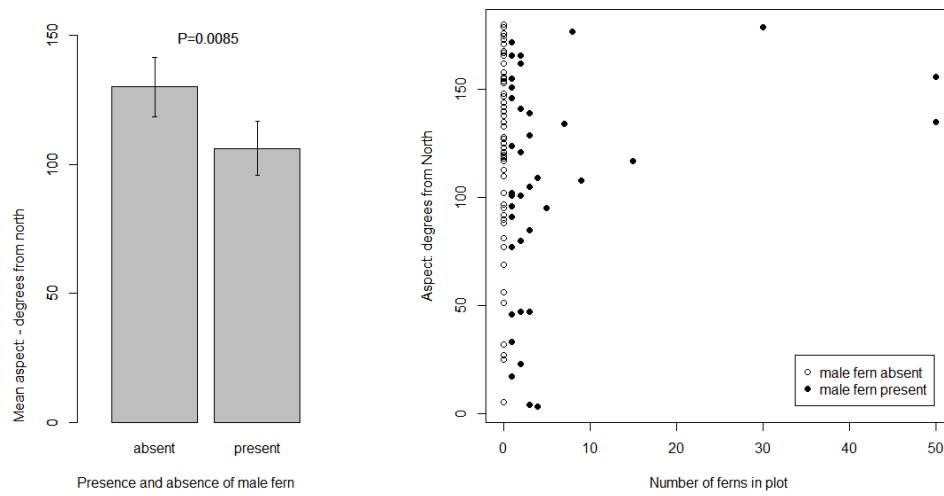


Figure 3.26 Mean aspect: degrees from north for plantation plots with and without *D. filix-mas* (left) and a scatterplot that shows how these plots are distributed by aspect. The majority of plots with *D. filix-mas* are between 75° and 180° (ENE/WNW – S)

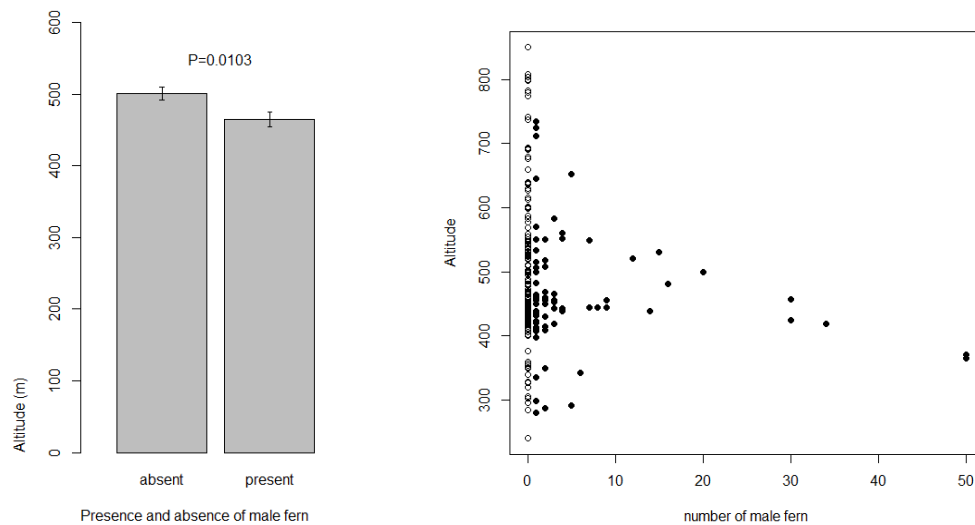


Figure 3.27 The relationship of foothills and inland plots with *D. filix-mas* relative to altitude (m).

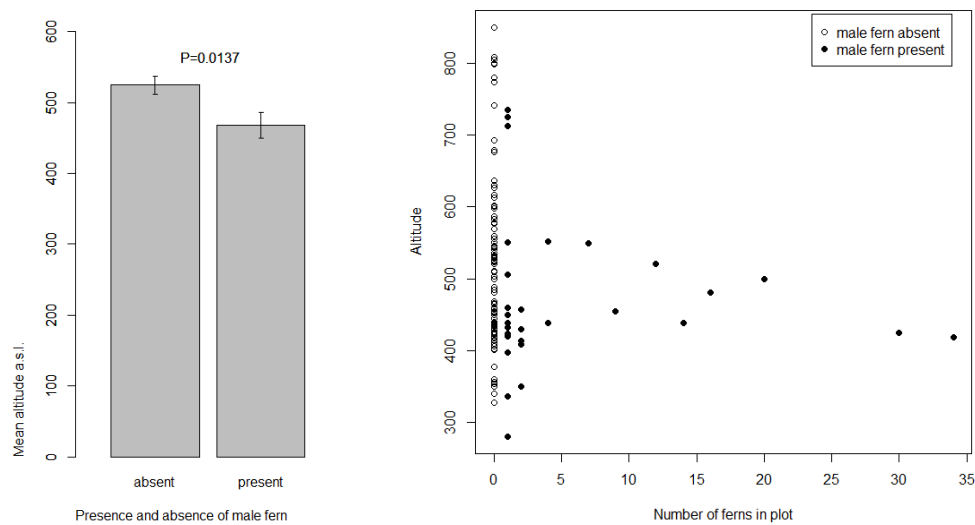


Figure 3.28 The relationship of *D. filix-mas* to altitude in the non-plantation plots.

The categorical variables (landform, aspect and land shape) were over-dispersed. However, when modelled with quasi-poisson shape gave a significant result, $P=0.0364$. This is presented in Figure 3.29 with contrasts between levels in Table 3.8 below.

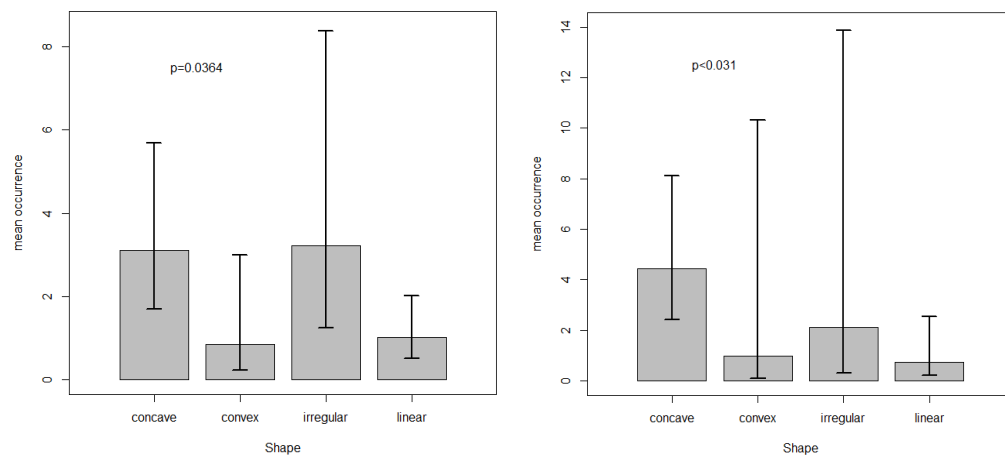


Figure 3.29 The mean number of *D. filix-mas* by land shape and after backtransformation from GLM of family: quasipoisson, resulting in the rather extreme error bars. The graph on the left represents all foothills and inland plots; with plantation plots on the right.

With the complete dataset, concave and irregular plots have an equal abundance of *D. filix-mas* and significantly more *D. filix-mas* than the convex and linear plots. In the plantation plots the only significant difference is between concave and linear plots ($P=0.0121$). Both convex and irregular surfaces have very different means from

concave surfaces but with small sample sizes are statistically unreliable (as can be seen in Table 3.9).

Table 3.8 Contrasts of the land shape levels using releval in R

| Levels compared | foothills | plantation |
|--------------------|--------------|------------|
| Concave-Convex | 9.54e-14 *** | 0.2286 |
| Concave-Irregular | 0.784 | 0.4664 |
| Concave-Linear | < 2e-16 *** | 0.0121 * |
| Convex - Irregular | 1.23e-11 *** | 0.623 |
| Convex - Linear | 0.293 | 0.820 |
| Linear - Irregular | 4.05e-15 *** | 0.357 |

Landform and aspect are not significant in this case but in Figure 3.30 below, similar patterns to those from Tiromoana Bush (Figure 3.13), which gave a significant result, can be seen, while the value for NW may be an anomaly caused by the comparatively small sample size. In reviewing the field data, most of the north, north east and north west plots with *D. filix-mas* are either in sheltered sites (gully floors, damp sites or sites of very little slope). Or it may be due to the large variation in sample sizes as shown in Table 3.9 below.

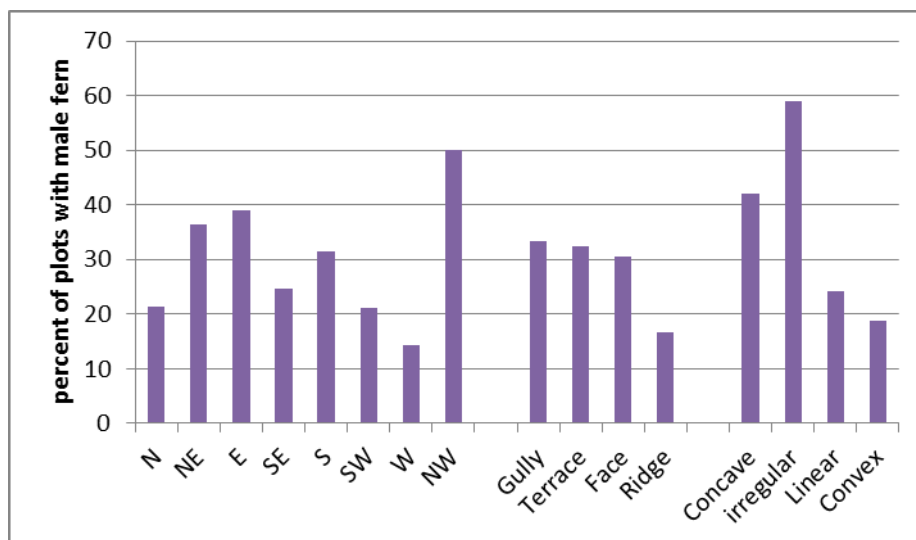


Figure 3.30 Percentage of plots in each category that contain *D. filix-mas* from all foothills and inland sites.

Table 3.9 Summary of the occurrence of *D. filix-mas* with aspect, landform and landscape for foothills and inland plots and the subsets plantation and non-plantation

| | Plantation | | Non-plantation | | Foothills and inland | |
|-------------------|-----------------|---------------------------|-----------------|---------------------------|----------------------|---------------------------|
| | Total plots (n) | % of plots with male fern | Total plots (n) | % of plots with male fern | Total plots (n) | % of plots with male fern |
| Aspect | | | | | | |
| N | 4 | 75 | 10 | 0 | 14 | 21 |
| NE | 6 | 50 | 15 | 33 | 22 | 36 |
| E | 21 | 62 | 17 | 18 | 41 | 39 |
| SE | 40 | 25 | 36 | 28 | 81 | 25 |
| S | 28 | 21 | 35 | 31 | 70 | 31 |
| SW | 4 | 50 | 13 | 15 | 19 | 21 |
| W | 2 | 0 | 4 | 0 | 7 | 14 |
| NW | 4 | 50 | 4 | 50 | 10 | 50 |
| Landform | | | | | | |
| Gully | 5 | 40 | 11 | 36 | 18 | 33 |
| Terrace | 20 | 45 | 10 | 20 | 34 | 32 |
| Face | 74 | 31 | 101 | 27 | 187 | 30 |
| Ridge | 9 | 44 | 12 | 0 | 24 | 17 |
| Land shape | | | | | | |
| Concave | 36 | 53 | 18 | 22 | 57 | 42 |
| irregular | 8 | 0 | 11 | 0 | 22 | 59 |
| Linear | 54 | 24 | 75 | 24 | 137 | 24 |
| Convex | 11 | 18 | 30 | 17 | 48 | 19 |

3.5 Discussion

The Tiromoana Bush dataset is the most comprehensive set of data collected from any one site during this study. As such it provides the most reliable information about the preferences of *D. filix-mas* in North Canterbury. The DCA ordinations for all tiers showed clear gradients for light permeability (measured by proxy with a densiometer) and soil moisture indicated by species typical of damp sites. *D. filix-mas* itself, is positioned away from hot, dry sites but is otherwise not particularly grouped with other species. By contrast the combined tiers ordination for the foothills and inland sites gave similar results, with light permeability, species diversity and canopy height having the strongest relationship to axis 1, which again was the only axis significant for *D. filix-mas*.

For Tiromoana Bush the primary axis produced by the groundcover ordination is significant for the presence of *D. filix-mas* ($P = 0.0018$), but a pattern specific to *D. filix-*

mas could not be discerned unless it is that it is widely associated with the other species encountered excluding those in Group 2 in Figure 3.9. With the foothills and inland groundcover ordination, all axes were significant for *D. filix-mas* suggesting a strong relationship with the distribution of other species. This ordination placed *D. filix-mas* firmly amongst the bulk of introduced herbs and grasses with a few indigenous plants characteristic of disturbance and edges such as *Haloragis erecta* and *Epilobium* spp, and several small shrubs and lianas (*Hebe leiophylla*, *Hebe traversii*, *Aristotelia fruticosa*, *Melicytus alpinus* s.l., *Coprosma propinqua*, *Sophora microphylla*, *Parsonsia capsularis*, *Rubus schmidelioides*, *Muehlenbeckia complexa* and *M. australis*) as well as several ground ferns (*Asplenium appendiculatum*, *A. flabellifolium*, *A. hookerianum*, *Blechnum penna-marina*, *Polystichum richardii*, and *P. vestitum*). All of these species are commonly found on sites of medium to high fertility although a few such as *B. penna-marina* can also be found on low fertility sites.

The graphs displaying the distribution of plots with *D. filix-mas* against the ordination axes, Figure 3.10, Figure 3.21 (reproduced below in Figure 3.31), Figure 3.22, also indicate that based on floristic similarity there are many plots within the rudimentary boundary that would be suitable for *D. filix-mas*. I can only speculate as to why *D. filix-mas* is not present although I suspect that propagule pressure and competition are major factors. It is my expectation that over time more of these plots will have *D. filix-mas* present and that some of the plots outside the drawn boundary will also have *D. filix-mas* present.

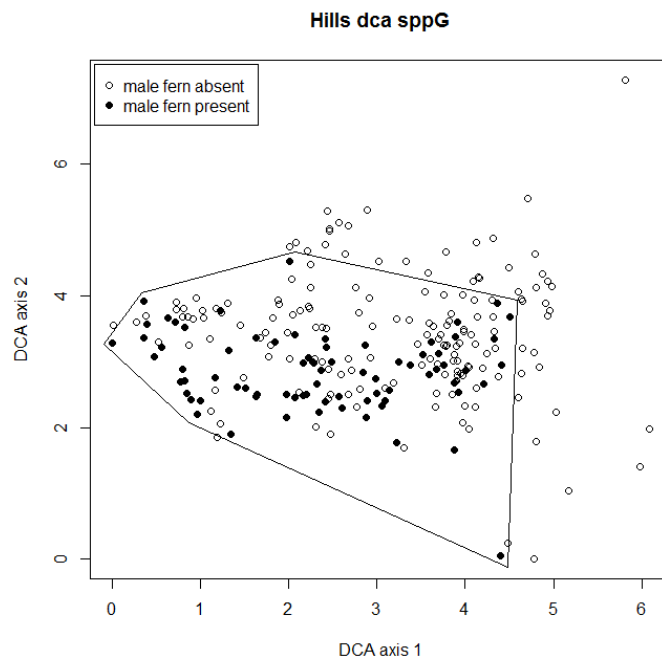


Figure 3.31 Distribution of plots with *D. filix-mas* from the foothills and inland site groundcover ordination. The drawn boundary provides a rudimentary indicator of plots which are likely to be suitable for *D. filix-mas* establishment based on their floristic similarity.

At Tiromoana Bush aspect, landform and shape are all significant predictors of *D. filix-mas* presence whereas with the foothills data only aspect and land shape are significant. It may be that climatic differences render landform less relevant in the foothills sites but I suspect that the lack of significance is due to the disparity of sample sizes between levels and anomalous records where *D. filix-mas* was encountered in sites with atypical shelter or soil moisture allowing establishment in a microsite. In both datasets *D. filix-mas* is most abundant on south trending aspects and declines as north exposure increases. Hollows in the landscape (gullies, concave surfaces, pits and uneven surfaces) are more likely to house *D. filix-mas* while exposed sites such as convex faces and ridges are less likely to support *D. filix-mas*. *D. filix-mas* was not observed in waterlogged sites although it was observed perched in wetlands, on stumps and on *Carex secta* trunks as well as in the narrow well-drained ecotone where seeps and streams give way to very dry conditions.

Light permeability of the canopy is not significant at Tiromoana Bush but is significant with the data for the foothills and inland sites that are non-plantation. All plots at Tiromoana are under kanuka and most of these are maturing kanuka which has a light canopy. In Figure 3.24 it can be seen that the negative effect on *D. filix-mas* is limited to

a permeability of less than 7%. This same scatterplot also shows the relationship with species diversity; *D. filix-mas* is favoured by the same conditions as those that favour having many different species in the groundcover of a plot. At Tiromoana Bush there was no relationship with species diversity. This may be attributable to the various seral stages present and in addition Henshaw (2012) reported that woody species at Tiromoana Bush are limited by both seed sources and dispersal. Consequently the full range of species that could be present at a site, given current conditions, may not be.

Altitude is the final factor that emerged as significant for *D. filix-mas* in the foothills and inland sites. The apparent and significant decline in occurrence above 600m may be due to less favourable conditions (temperature, length of growing season, rainfall, fertility and pH), it may still be a random effect (there were not many plots over 600m) it may be due to less disturbance, or it may be due to competition as the higher rainfall with altitude increases the density of established groundcover. In Chapter 4, I will report the highest record from New Zealand as 1200m in the McKenzie district and I am aware of unverified but reliable reports from near treeline (c. 1300m) in the upper South Island.

Canopy height, slope and canopy intactness (gaps) are poor predictors of *D. filix-mas* with all datasets.

With regard to invasiveness it appears that *D. filix-mas* is invasive in some situations in North Canterbury, namely where a site has been degraded, anthropomorphic disturbance has occurred or in seral forest ecosystems such as can be found under kanuka succession. The altered fertility that also comes on farm and ex-farm sites may be a contributing factor to the apparent success of *D. filix-mas* (and other exotic plants) in retired sites. In terms of the definition for invasive given in Chapter 1, it could be argued that *D. filix-mas* is not 'detrimental' in forest plantations however the apparent high numbers at forest margins may prove detrimental to indigenous remnants within the plantation and adjacent indigenous dominated habitats because of the increased propagule pressure this will create. In this study undisturbed forests of black and red beech appear to be quite resistant to *D. filix-mas* incursion except when the forest is part of a current or past farm operation.

In summing up the analysis shows that in North Canterbury, *D. filix-mas* is more likely to be found on lowland to montane sites up to 600m that are fertile, well-drained, not

simultaneously both hot and dry, are low in the landscape or have a shape that offers shelter (hollows rather than humps) and with an aspect between 75° and 285° True. The canopy species is not critical but *D. filix-mas* is most likely to be found under kanuka, exotic softwoods and deciduous hardwoods, brush weeds and grey scrub but not under montane indigenous beech forest that has not been degraded. Provided a suitable spore source is available *D. filix-mas* can be expected to establish under light shelter that harbours other exotic species, or sites degraded by human activity or pastoral farming.

4 Chapter 4 National distribution, range of observed habitats and the potential extent within New Zealand using Land Environments New Zealand.

4.1 Introduction

The known distribution of *D. filix-mas* in New Zealand has not been previously mapped. This chapter brings together the bulk of New Zealand records and maps these against the Level IV Environments from the Land Environments New Zealand (LENZ), 2002 dataset (Leathwick et al. 2002, 2003), to give an indication of the potential extent of *D. filix-mas* based on the environments occupied by these records. The results and discussion delve further into some of the variables in the LENZ dataset in relation to the extent of *D. filix-mas* and also limitations with the dataset and its resulting reliability.

4.2 Method

National records for *D. filix-mas* were collated from four New Zealand herbaria: Auckland War Museum (AK), Museum of New Zealand – Te Papa Tongarewa Herbarium (WELT), University of Canterbury Herbarium (CANU) and from the Allan Herbarium (CHR) at Landcare Research, Lincoln. Unverified reports were obtained from the Department of Conservation's, BioWeb database, the New Zealand Biodiversity Recording Network (NZBRN) and from nationwide botanical society field lists collated by Graeme Jane. Most contributors to these latter two are professional botanists or ecologists. Further records were obtained by myself and a small team of volunteers who sent in either vouchers or photographs with GPS co-ordinates during their travels over a three year period. A representative sample of records was also incorporated from the study sites in North Canterbury. The ad-hoc manner in which these records have been collected makes statistical analysis impractical; in particular the high concentration of records from Canterbury may be due as much to the high concentration of botanists and ecologists in this area.

Co-ordinates came in several forms (NZMS 1 map grid, NZMS 260 map grid, NZ Geodetic Datum and NZ Transverse Mercator) which were transformed into Longitude and Latitude (decimal degrees) using Land Information New Zealand's "Online Conversions" tool for import into the 'ArcGIS' geospatial information system (GIS) software package.

The LENZ layers and maps provide a framework for identifying similar growing environments across New Zealand, irrespective of their geographical location on the basis of selected predictive climate, topography and soil attributes/limitations.

Environments are presented in four hierarchical levels in raster layers with a nominal spacing of 25m x 25m at Level IV (1:50 000 scale). The Level IV Environments are used here because even with this limited set of records there are clear separations with respect to the occurrence of *D. filix-mas*. While there are advanced options for working with the LENZ data, in this instance it has been used simply to obtain a table of Level IV environments and the associated predictive data that are overlain by the record points. From this, potential extent is mapped and some summary data is presented. As mentioned above not too much should be inferred from averages and medians rather the overall range of sites may be instructive.

4.3 Results

The combined points from all sources came to 357 including 38 from study sites used in Chapter 3 and are shown in Figure 4.1. *D. filix-mas* is recorded from Auckland City, east to the western flanks of the Urewera, through the central and western parts of the North Island to Wellington. It has not been recorded from Northland, East Coast (1 historic record), Hawke's Bay or Wairarapa. In the South Island it has been recorded from the Tasman/Nelson area and sporadically throughout the eastern side of the island all the way to Bluff on the southern coast. There are a very few records from the West Coast and these are generally in close proximity to towns. It has not been recorded from Fiordland proper, South Westland or the Tasman Mountains and Golden Bay. While most records are from lowland to montane levels, the lowest are near sea level and the highest reported is at 1200m in the MacKenzie district, north of MacKenzie Pass. Records come from high and low rainfall areas, and from ancient acidic soils (Moutere Gravel in Tasman) to recent basic soils (limestone talus in the Clarence Valley).

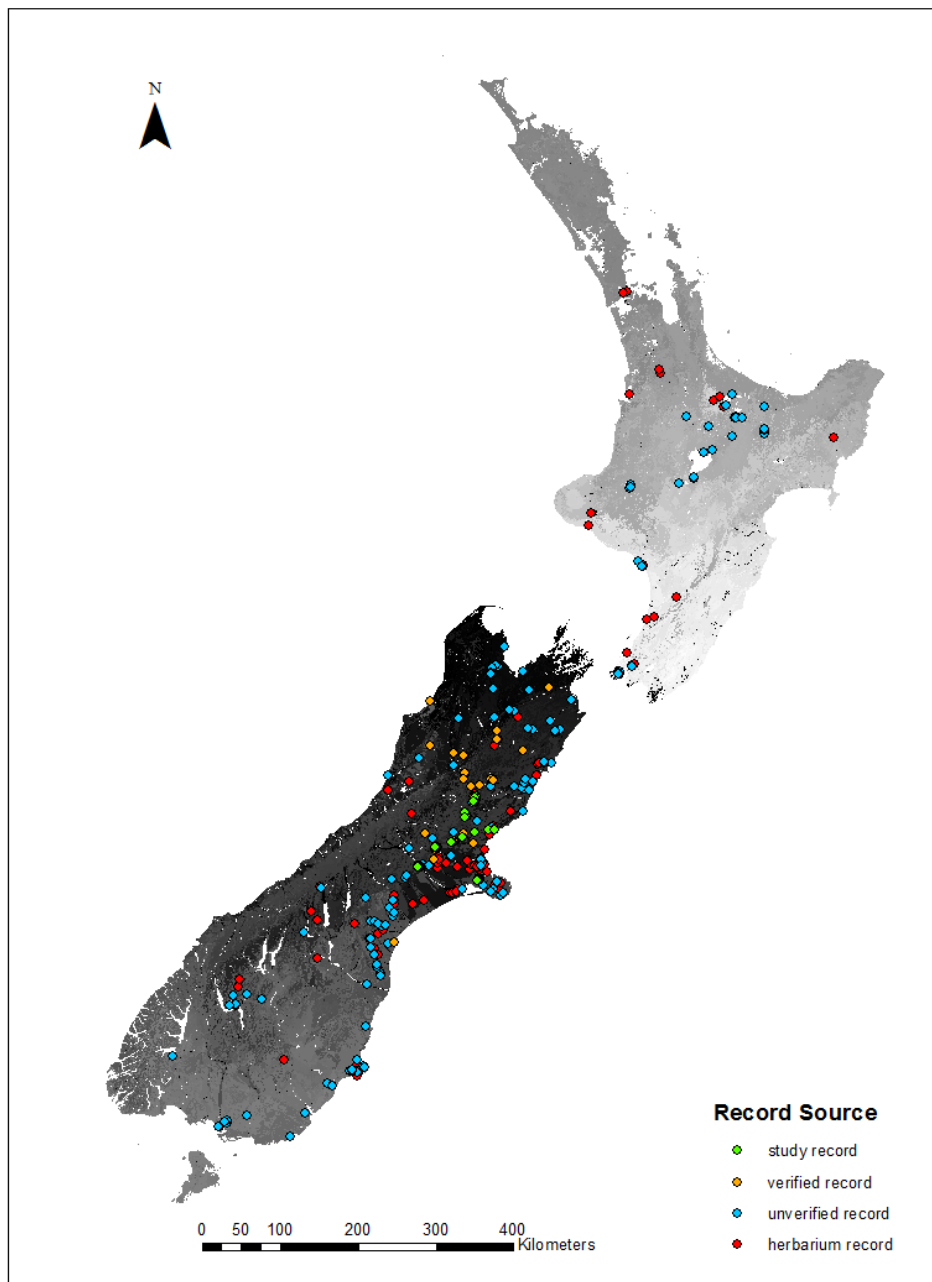


Figure 4.1 357 records of *D. filix-mas* from New Zealand, many are overlain by adjacent points at this scale. Unverified records are those for which there is no reference to a voucher or photograph with which to verify the record, although the identification is from a reliable source e.g. Colin Meurk and Peter de Lange.

Table 4.1 gives a brief overview of the potential proportional land area available to *D. filix-mas*, as interpreted from its occurrence in environments at each of the four LENZ Levels. At LENZ Level I – 90 percent of New Zealand may be suitable for *D. filix-mas* with just three terrestrial environments in which it has not been reported. These are D,

G and S (T is permanent snow and ice). Working through the Levels the proportion of New Zealand suitable for *D. filix-mas* decreases to 57 percent at Level III and 38 percent at Level IV being the environments reported to contain *D. filix-mas*.

Table 4.1 Indicative proportion of New Zealand susceptible to colonisation by *D. filix-mas* as determined by known occurrence within LENZ environments at the four levels of Land Environments New Zealand

| | Land Environment level | | | |
|---|------------------------|----------|-----------|-------------------|
| | Level I | Level II | Level III | Level IV |
| Number of Environments in Level | 20 | 100 | 200 | 500 |
| Number of environments with <i>D. filix-mas</i> | 17 | 42 | 88 | 105 |
| Percentage of NZ in sampled environments | 90% | 60% | 57% | 38% |
| Land Area out of 26. 225 million ha | — | — | — | 10.050 million ha |

In Table 4.2 and Table 4.3 summary attribute data are presented for all the LENZ Level IV environments, alongside summary attribute data for the environments in which *D. filix-mas* is reported. The full table of data with each of the 105 environments in which *D. filix-mas* is reported is presented in Appendix 0. Temperature and solar radiation do not appear to have an influence on *D. filix-mas* but October Vapour Pressure Deficit (VPD), Monthly Water Balance and Monthly Water Deficit may be informative and are also correlated. *D. filix-mas* is not reported from areas with very low VPD (humid), very high water balance (1.3 – 9 compared to 0.9 – 22.8) or areas with the highest water deficit -274mm compared to -320mm.

Table 4.2 and Table 4.3 summary elevation and climate data of the LENZ Level IV attributes as taken from the attributes table for the Level IV raster file. The minimum and maximum values for all 500 of the Level IV environments are presented first, followed by comparative data for the 105 environments in which *D. filix-mas* has been recorded.

| | Elevation | Annual Temp | Minimum Temp | Annual Solar Rad | Winter Solar Rad | October VPD | Water Balance | Water Deficit |
|--|-----------|-------------|--------------|------------------|------------------|-------------|---------------|---------------|
| Min all environments | 4 | 2.5 | -4.6 | 11.7 | 2.7 | 0 | 0.9 | 0 |
| Max all environments | 1859 | 15.8 | 8.5 | 15.4 | 7.1 | 0.64 | 22.8 | 320.52 |
| Min <i>D. filix-mas</i> environments | 5 | 4.6 | -4.5 | 12.2 | 3 | 0.23 | 1.3 | 0 |
| Max <i>D. filix-mas</i> environments | 1508 | 14.9 | 6.7 | 15.3 | 6.3 | 0.62 | 9 | 274.07 |
| Median <i>D. filix-mas</i> environments | 260 | 10.7 | 0.9 | 14.0 | 4.6 | 0.39 | 2.6 | 46.7 |
| Mean <i>D. filix-mas</i> environments | 345 | 10.5 | 0.8 | 14.0 | 4.5 | 0.40 | 3.0 | 68.1 |

| | Slope | Drainage | age | Chem_limitations | Acid_sol_P | Exch_Calcium | Induration | Particle_size |
|--|-------|----------|-----|------------------|------------|--------------|------------|---------------|
| Min all environments | 0 | 0.7 | 0.3 | 0.1 | 0.4 | 0.1 | 0.6 | 0.6 |
| Max all environments | 42.9 | 5 | 2 | 3 | 5 | 4 | 5 | 5 |
| Min <i>D. filix-mas</i> environments | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Max <i>D. filix-mas</i> environments | 31.3 | 5 | 2 | 2 | 5 | 4 | 4 | 5 |
| Median <i>D. filix-mas</i> environments | 5.6 | 5.0 | 2.0 | 1.0 | 3.0 | 1.9 | 3.1 | 2.9 |
| Mean <i>D. filix-mas</i> environments | 8.8 | 4.4 | 1.8 | 1.0 | 3.0 | 1.7 | 2.9 | 2.7 |

D. filix-mas is not associated with environments with a mean slope greater than 31.3° which can be interpreted as environments too steep for soil accumulation.

Chemical limitations refer to salinity(2) and ultramafic (3) and *D. filix-mas* is found in environments with mean values from 1 – 2 the latter being a single record from the margin of Lake Ellesmere in Canterbury.

The remaining soil categories are all correlated to some degree. Induration and particle size affect the availability of phosphorous (P) and calcium (Ca) in that hard rock and a lack of fine material limit these minerals and other cations such as potassium. *D. filix-mas* is not generally associated with environments characterised by parent material that is both massive and hard wearing or has very low levels of P or Ca; acid soluble P is shown in Figure 4.3 which shows that the eastern South Island has relatively high P compared to eastern North Island but *D. filix-mas* appears to occur on much lower P sites in the volcanic regions. However, in looking at the latter sites in close-up most of these are in localised sites of higher P (Figure 4.2)

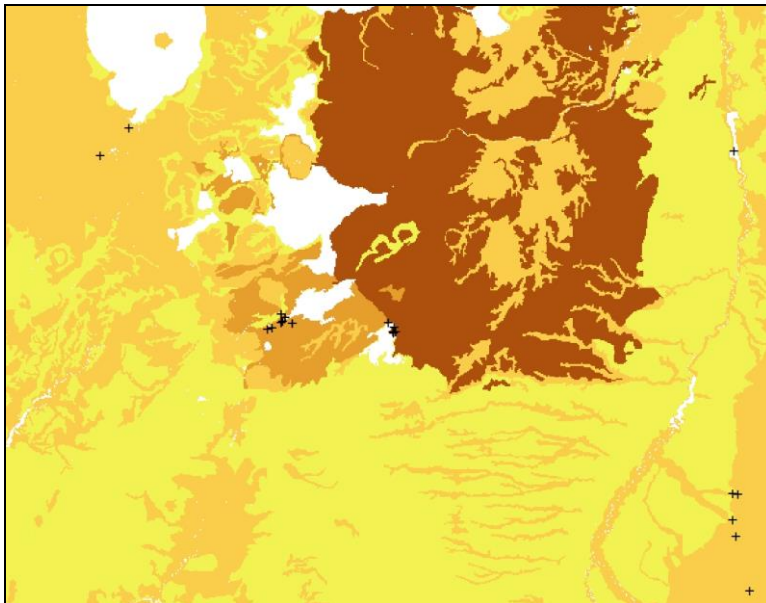


Figure 4.2 Close-up from Figure 4.3 showing that records are not on the very low P sites. This area covers from Roturua in the top left to Murupara in the bottom right.

A number of Level II, III and IV environments featured prominently for *D. filix-mas*. These environments are presented in Table 4.4 with a brief description. They can be characterised as ranging from near sea level to alpine; from the Bay of Plenty to Southland, from flat to steep; moderate to well drained; moderate to high fertility (some

low); high to low vapour pressure deficits high to low water deficits and most are in the South Island.

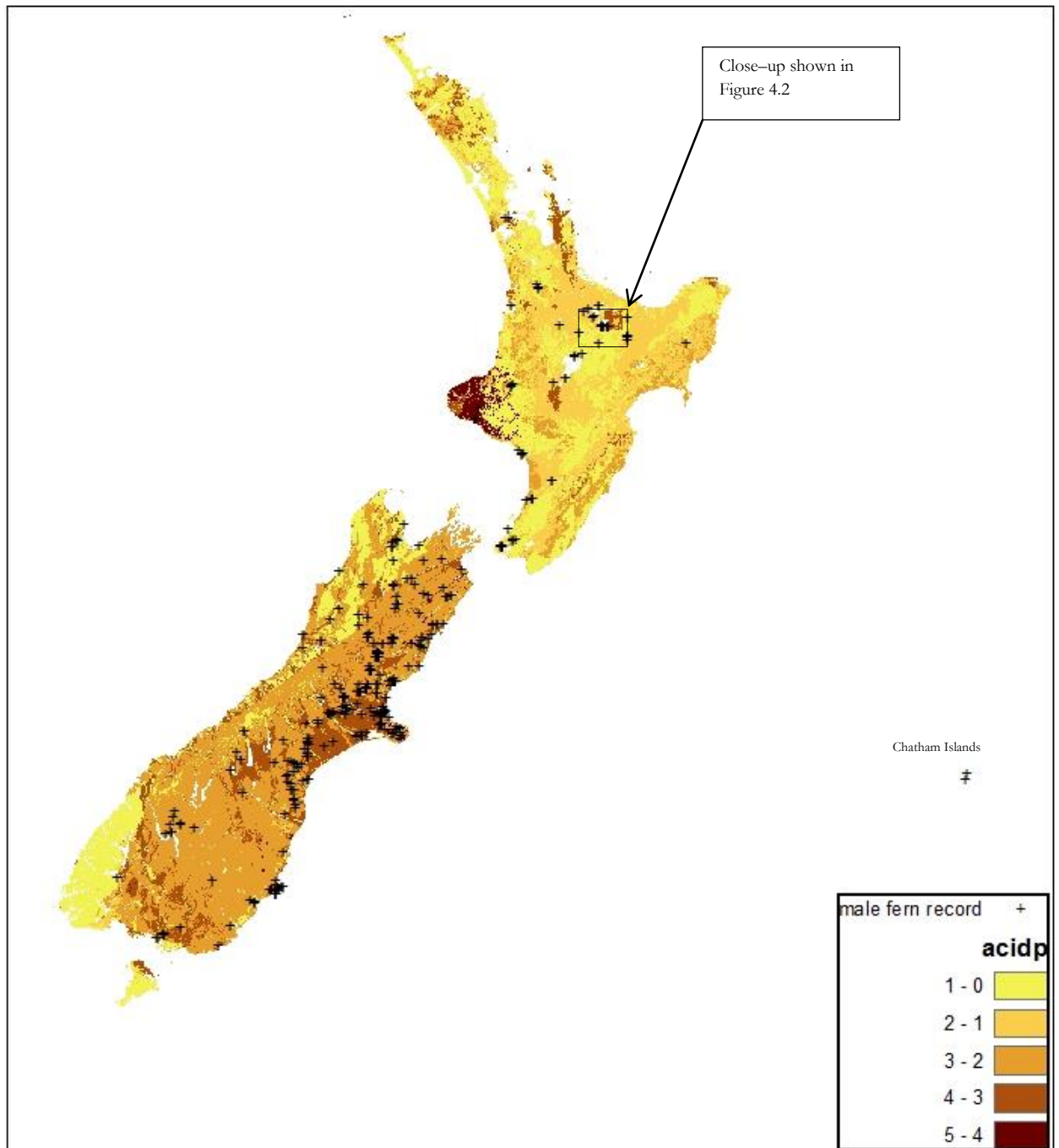


Figure 4.3 Acid soluble phosphorous from the LENZ underlying data. The scale ranges from < 7 mg/100 g (1 - 0) to 100 - 60 mg/100 g (5 - 4). Note the two records on the Chatham Islands (not included in LENZ)

Table 4.4 Principal LENZ environments containing *D. filix-mas*

| Environments | | Number of records | Main localities | Description |
|---|---------------------|-------------------|--|---|
| Level I | Unique environment | | | |
| B - Central Dry Lowlands | B3 | 24 | North Canterbury | VPD high, easy hills, moderate drainage, moderate fertility |
| E - Central Dry Foothills | E1, E3, E4 | 90 | Steep hills on Eastern S. Island | VPD high, steeper hills, well drained of moderate fertility E1 includes foothills in Central Hawkes Bay |
| F – Central Hill Country and Volcanic Plateau | F1.4 | 10 | Wellington and Wairarapa | VPD moderate, imperfect drainage, low fertility |
| F | F3 | 20 | Banks Peninsula | VPD moderate, imperfect – well drained, moderate – high fertility |
| F | F6, F7 | 20 | Volcanic Plateau Coromandel | East to Gisborne and Hawkes Bay well drained, low fertility defined by rhyolitic ash. F7 can have severe frosts |
| H – Central Sandy Recent Soils | H2 | 11 | Rotorua and Urewera | VPD moderate, imperfect - well drained, moderate fertility from tephra and sandstone |
| J - Central well drained recent soils | J2.1b (Level IV) | 6 | Marlborough and Christchurch | VPD high, well drained, high fertility flood plain soils |
| J | J4.2 | 4 | Manawatu Wanganui | VPD moderate, well drained, moderate fertility coastal sand and Taupo tephra |
| K – Central upland recent soils | K1.1 | 9 | Eastern Southern Alps | VPD moderate, well drained, high fertility alluvium and loess in main headwaters |
| N – Eastern South Island Plains | N1, N2, N3 | 66 | Canterbury, North Otago and Northern Southland | VPD moderate to high, imperfect – well drained, mostly of high fertility on flat to undulating plains of alluvium and loess |
| P – Central Mountains | P1 & P2 | 11 | Nelson south to North Otago | VPD low – moderate, imperfect – well drained, low – moderate fertility. High altitude, steep and high rainfall. |
| Q – Southeastern hill country | Q2 | 13 | South Canterbury - Southland | VPD moderate, low water balance, imperfect drainage with schist and good drainage on greywacke, moderate fertility. Steep montane slopes of inland ranges |

4.4 Discussion

D. filix-mas is widespread through the eastern South Island and scattered through the western and central parts of the North Island. It has not been recorded from Stewart Island, where it is unlikely to self-introduce due to the prevalence of south and west winds. It is also not recorded from Fiordland, South Westland and the central alpine spine of the South Island, with the exception of 1 record near Mt Cook village and another beside the road on the Arthur's Pass. However there are scattered records in the lesser mountains north of the Hurunui River, which is consistent with the indications from the LENZ data that *D. filix-mas* is not found in environments with extreme rainfall, overly steep landforms and very hard parent material - all of which prevent formation of a fertile soil. Low fertility might also contribute to the absence of records from East Coast, Hawkes Bay, Manawatu Bush and Wairarapa. A single 1949 record from the East Coast only has a map sheet which puts in the vicinity of Matawai and this has been marked accordingly, however that record has very little effect on the predicted extend of *D. filix-mas*. North Island records are largely associated with volcanic or sandy soils with low – moderate fertility. Only a few around Wellington are associated with sedimentary rock types. On the west coast of the South Island *D. filix-mas* records are all north of Hokitika and from relatively low rainfall areas (valley floors and coastal). They are also, all in close proximity to towns or alongside roads.

The big question is: are these records representative of reality? Followed by: is *D. filix-mas* really most abundant in Canterbury? And are the gaps real or are they a product of observer effort and bias? The latter is in particular regard to the eastern North Island, central Southland and inland Otago gaps. Canterbury, Wellington and Waikato, have a concentration of professional botanists and ecologists due to the universities and science institutions in these areas, which may result in higher reporting. In contrast, absence of a record does not mean plant absence, particularly in remote and mountainous locations which are seldom visited or traversed off the well-trodden paths by a person who would notice and report the occurrence of weeds.

Before discussing the results from overlaying these points onto LENZ layers it is necessary to briefly discuss the limitations of the LENZ data layers.

The rationale behind the choice of data, how the data layers were extrapolated across the New Zealand landscape, the limitations of the data and the validation processes undertaken are discussed in detail in the *Land Environments of New Zealand* (Leathwick et al. 2003) and the *Land Environments of New Zealand Technical Guide* (Leathwick et al. 2002). The primary purpose was to predict pre-human vegetation cover in a way that is not constrained by geographic boundaries such as catchments or political and management units such as counties, reserves etc. What LENZ doesn't do, is describe environments in terms of their potential following anthropomorphic change, which in this study, is about altered drainage, fertility and disturbance.

The different data layers are mapped at different scales in the source data and the scale of accuracy over the country varies within the layers, depending on the quality of the data available. In essence, areas of higher human importance have better data than remote areas of low human importance. Therefore, while I have used Level IV here with raster points on a 25m x 25m grid the accuracy will, over most of the country, be somewhat less and even at this scale, microsites are not identified even where the data set is reliable. Tied to this is the absence of a layer incorporating aspect which has a big effect on solar radiation and as a consequence soil and daytime air temperature and soil moisture (Water Balance and Water Deficit in Table 4.2). Despite reliability issues LENZ provides a useful framework in which to identify areas of similar ecological potential or as in this case, come to a better understanding about an organism in the New Zealand environment.

Despite the uncertainties with both the *D. filix-mas* records and reliability of the underlying data, LENZ remains informative and has facilitated the creation of an indicative map of land where *D. filix-mas* may be expected to grow given the opportunity (Figure 4.4). In the North Island *D. filix-mas* is currently associated with volcanic, alluvial and sandy soils with a scattering of suitable sites in East Coast and Northern Hawkes Bay but is more concentrated from Southern Hawkes Bay to Wairarapa and through much of eastern Taranaki, Wanganui, the Volcanic Plateau and east along the flanks of the Urewera and Raukumara Ranges. In the South Island it is only the wettest, highest and more remote areas in which *D. filix-mas* has not been reported. The main favourable soils are alluvium, loess, and talus or are weathered directly from soft, calcareous, sedimentary rocks. This is correlated with the absence of reports from

environments that are steep, although having seen *D. filix-mas* growing on rock faces, vertical alluvial banks and masonry walls it may be as much that difficult terrain is seldom visited.

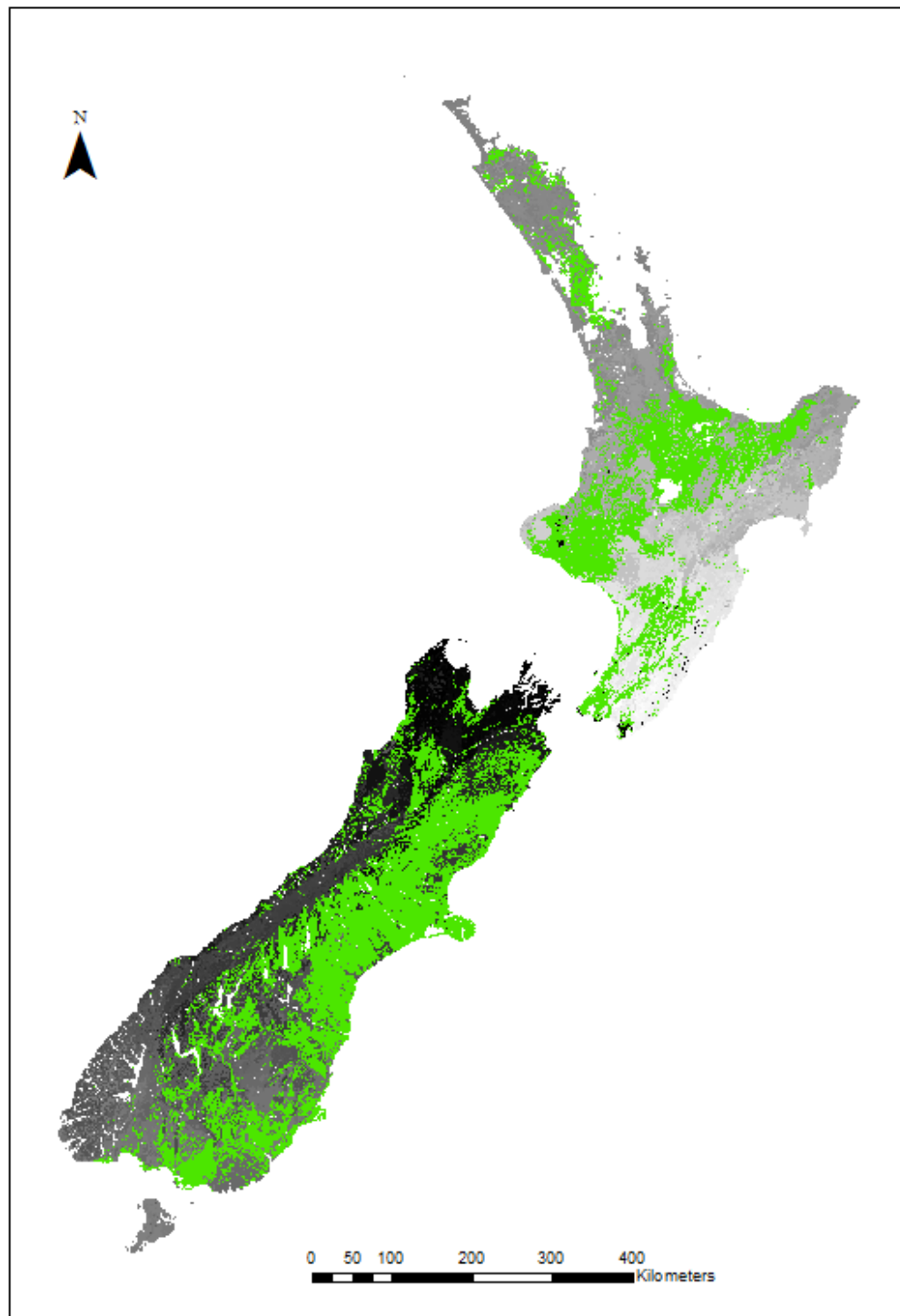


Figure 4.4 Land Environments recorded as containing *D. filix-mas* (green) demonstrating the wide potential for this fern in New Zealand.

At Level I all environments are suitable except Environments D, G and S. Environment D is steeper hill country from the northern half of the north island and includes most of the hill country around the East Cape south to Napier. There is nothing inherently obvious that would make this environment unsuitable for *D. filix-mas*.

Environment G is rare but widespread over the upper half of the North Island being recent soils of either sand (dunes) or lowland river flood plains. Fertility is moderate to low and drainage moderate to poor. Of the Level II G Environments: G2, G3 and G4 would be best suited to *D. filix-mas* with some limitations.

Environment S is the ultramafics, there is nothing in the literature to indicate that *D. filix-mas* can tolerate ultramafic conditions and *D. filix-mas* has opportunity to establish on the Dun Mountain ultramafic complex from ferns in Nelson City if ultramafics are suitable. There is one record in the data from a saline environment at Lake Ellesmere, however as mentioned above LENZ tends to brush over micro-sites and I suspect that this record is either misplaced or in a non-saline micro-site. The record must stand as it is, but should not be taken to indicate from this one record that *D. filix-mas* is tolerant of saltmarsh conditions.

There is a large difference in the area suitable for *D. filix-mas* when comparing Level III and Level IV environments, I suspect the actual area that is suitable for *D. filix-mas* colonisation will lie somewhere between these two i.e. between 35 and 60 percent of New Zealand. On the one hand there are parts of environments that will be unsuitable e.g. in Environment E where north aspects will be too dry, but this is countered by the reverse situation and most importantly, the absence of a record does not constitute a negative result. Consequently there will be quite a few land environments that are suitable or already have *D. filix-mas* but are not included because it has not yet been reported. *D. filix-mas* is excluded from many areas by current management practices e.g. the bulk of the Canterbury plains, but can quickly enter when management is favourable e.g. change from pastoral to exotic forestry or altered fertility as a result of management practices or anthropogenic disturbance.

There are no records north of Auckland City but the three records from Auckland City result in the inclusion of areas throughout Northland (Environments A6 and A7) in Figure 4.4 however it is not clear what relationship the sites now have to the LENZ

environments or whether these ferns are truly wild or cultivated, consequently the inclusion of Northland should be treated with caution but not altogether disregarded.

Central and Southern Hawkes Bay are very similar to Canterbury and Marlborough yet have no records for *D. filix-mas*. The only explanation for this from the underlying data comes in the form of comparatively low phosphorous (Table 4.3 and Figure 4.3), however even if this is true, agricultural practices have long since altered the levels of P and Ca and I expect the absence of records is more likely to be due to either a lack of collection effort or an absence of domestic plants from which to establish wild plants.

Climatically winter minimums have no effect but annual temperature may, with *D. filix-mas* not recorded from 13 land environments with an annual mean temperature less than 4.6°C. These encompass all the higher mountains of the South Island from Fiordland to the Richmond Ranges including the crests of the Tasman Mountains and uplands of the inland Otago and Canterbury ranges such as the Rock and Pillar, Eyre and Hawkdun Mountains. In the North Island it includes the higher parts of the volcanic cones, but not the Tararua or Ruahine Ranges, however winter temperatures have no effect. The correlation with very low October VPD excludes 63 mountain land environments at lower altitude in Fiordland, the Southern Alps, North Island mountains and around the volcanic cones, particularly the west side of Taranaki; many of these environments also have low fertility and have either impeded drainage or are permanently wet. Low October VPD is also correlated with Water Balance where 36 of the same land environments have a monthly water balance ratio greater than 9.0 which is the maximum for any land environment where *D. filix-mas* has been recorded. What is not clear is whether the correlation is due to low VPD and high rainfall being unsuitable for *D. filix-mas*, or if this is more about a low human population, consequent low or no introduction of *D. filix-mas* and biotic resistance from the dense and prolific growth of extant species in the high rainfall areas.

Water deficit also appears to limit to some extent with *D. filix-mas* not recorded from the 5 environments with a mean annual water deficit greater than 274mm These are very dry terraces in Wairau, Awatere and Clarence catchments; coastal saline and non-saline soils from the Wairau River south to Lake Ellesmere; and Environment N8: the semi-arid saline and non-saline soils of Central Otago. I believe this overstates the aridity

tolerated by *D. filix-mas* and will use observations at Lake McRae in the Clarence Valley to illustrate this. Here *D. filix-mas* was seen at 4 separate sites in 2012, being very narrow bands of moist soil in gullies with some form of summer shade. These micro-sites are incorporated into Environment E4.1a but are in stark contrast to the surrounding E4.1a landform which borders on semi-arid and where the fern was not seen. E4.1a has a mean water deficit of 195mm but has a high fertility and at a mean altitude of 700m a.s.l. is relatively cool. The sites in which these ferns are growing would effectively have a negligible water deficit as soil water is replenished from the adjacent spring fed streams.

5 Chapter 5 Summary and Conclusions

5.1 Overview

In this thesis an extensive literature review of the ecology of *D. filix-mas* has been completed and further knowledge of its ecology in New Zealand determined by experiment and field survey. All valid records have been collated to produce a current distribution map and this information used to produce a potential national distribution through association with the LENZ Level IV environments. It is suggested here that *D. filix-mas* is an invasive species in degraded and anthropogenically disturbed sites in North Canterbury, capable of establishment across a wide range of climatic, altitudinal and geological gradients, and in a wide range of botanical associations. While relatively intact beech forest appears to be resistant, it is not proof to invasion by *D. filix-mas*.

5.2 Habitat requirements in North Canterbury

D. filix-mas occupies a wide range of habitats in New Zealand just as it does in the Northern Hemisphere. The shade experiment demonstrated that light availability is unlikely to limit survival of *D. filix-mas* in indigenous forest and the high plasticity of fronds exhibited across the treatments confirmed the findings of Bannister and Wildish (1982) that *D. filix-mas* is well adapted to a wide range of exposure. The field data analysed in Chapter 3 shows that in North Canterbury: aspect, altitude, landform, land shape, and light levels may influence the distribution and abundance of *D. filix-mas* in the landscape. *D. filix-mas* was not found on exposed north aspects and the analysis of inland and foothills sites suggests that very low light levels (less than 7% canopy porosity) may limit *D. filix-mas* in the wild. However in the shade experiment, plants gained in fresh weight in the darkest treatment (c. 96% shade), with the greatest growth at the lightest level of shade (69% shade). Plants in the fully exposed treatments had a poor response which contrasted starkly with the field situation where the least amount of shade was around 10% and complete loss of cover did not appear to affect the health of wild ferns. On the contrary at several sites (records used in Chapter 4) fully exposed plants were the most robust ferns encountered.

Ordinations with this data suggest that *D. filix-mas* is most commonly associated with other plants that prefer moderate – high fertility, moderate moisture and good drainage. It was also more likely to be encountered with other exotic species although at

Tiromoana Bush this was not so evident. While it can tolerate very dry conditions this is not usually in conjunction with very hot conditions.

D. filix-mas also showed a positive correlation with increase in species diversity in the foothills sites although at Tiromoana Bush it appeared to make no difference. It is probable that micro-sites favourable to a diverse range of species are also favourable to *D. filix-mas* rather than there being any causal link between the two.

5.3 Invasiveness and potential extent

D. filix-mas has the hallmarks of a serious invasive species: it tolerates a wide range of conditions, appears to be well-adapted to New Zealand conditions, grows alongside indigenous species of similar habit (in particular its near relatives *Polystichum vestitum* and *P. richardii*), and has numerous propagules (spores) that are dispersed widely (Butaye et al., 2001). During the collection of records it was observed that *D. filix-mas* often occurs in open clusters of fertile and sterile (immature) plants. These clusters occur at both the micro-scale and local scale. The bulk of ferns are separated by mere centimetres to a few metres in clusters with a few fertile plants, but can be out to 50 metres or more when many fertile plants are present. In remote areas clusters may be separated from other clusters by hundreds of metres (e.g. in the Clarence Valley) or by kilometres (Maruia and Wairau Valleys). It was also noted that in almost all situations where *D. filix-mas* occur singly without near neighbours these plants are young (sterile). These observations have not been tested but they do suggest that *D. filix-mas* is in a dispersal stage through Marlborough and Canterbury hill country, with considerable dispersal and population increase still to occur.

In Chapter 4 when comparing records of *D. filix-mas* with the Land Environments New Zealand classifications, *D. filix-mas* was found in all principal environments (Level I) except for - ultramafic, some very steep and hard-rock mountain environments and low fertility recent soils in the upper North Island. *D. filix-mas* has not been reported from environments with mean annual temperatures below 4.6°C or with very high rainfalls in combination with very low October vapour pressure deficits. It is also not reported from semi-arid and saline environments found in Marlborough, Canterbury and Otago but as demonstrated with the Lake McRae records, can be found in these drylands where supplementary fresh water is available in the ecotone between wetlands and

drylands. As with the European experience there does seem to be a correlation with reasonable fertility particularly nitrogen and phosphorous together.

With all this in mind *D. filix-mas* is unlikely to be a significant problem in that part of the mountains of the South Island, that fit between the Alpine Fault and the Main Divide, from and including Fiordland north to at least Arthur's Pass. Elsewhere it is unlikely to encroach much above treeline on the drier mountains, and while it may be found locally in the semi-arid parts of Marlborough and Otago, it is unlikely to become a major problem in these areas. In North Canterbury it appears that *D. filix-mas* is primarily invasive in degraded sites, riparian zones, south facing grey scrub, seral kanuka communities and exotic plantation, while intact beech forest is resistant, but not proof, to invasion by *D. filix-mas*. This study did not examine soil chemistry or barriers to effective dispersal. European data suggests that *D. filix-mas* is inhibited by low fertility (N,P,K) and low pH (Hill et al. 1999, Ellenberg and Leuschner 2010). It is possible that the low occurrence in undisturbed forest is due to lower fertility and lower pH. It may also be due to low propagule pressure combined with a high biotic resistance from indigenous species competing for the same sites. Intensive grazing, traditional firing of woody vegetation, top-dressing and oversowing will affect all these parameters in a manner conducive to giving *D. filix-mas* a foothold. Once established in an area, propagule pressure will increase and *D. filix-mas* may in time be able to overcome the apparent biotic resistance. Should this prove to be correct the map produced using LENZ (Figure 4.4,p86) gives a fair indication of the parts of New Zealand in which *D. filix-mas* could become common, covering nearly 40% of the New Zealand surface area.

5.4 Implications

D. filix-mas is most likely to have appreciable impacts on indigenous ecosystems east of the Main Divide of the South Island in areas that have a history of disturbance (e.g. fire and grazing) but are no longer subjected to disturbance. *D. filix-mas* has the potential to become a large part of the ground species on retired and regenerating lands and may become a factor for consideration when undertaking restoration of remnants, revegetation and extension of existing protected natural areas. Insufficient knowledge was gained in this study to comment on the North Island situation, however as with the South Island *D. filix-mas* is widespread and appears to be associated with past disturbance on soils with moderate to high phosphorous.

5.5 Recommendations

This thesis demonstrates that *D. filix-mas* is capable of establishing on at least 40% of New Zealand's land area (see Figure 4.4, p.86). Much of this area is currently farmed and intensive farming will limit *D. filix-mas* to marginal farmland, exotic forest, roadsides, riverbeds and riparian margins and the remaining pockets of indigenous dominated vegetation. Remnants whether protected or not are vulnerable to loss of indigenous biodiversity and the natural processes that foster biodiversity.

It would be desirable for *D. filix-mas* to be officially recognised as a weed throughout New Zealand with the sale, propagation and dissemination prohibited by including *D. filix-mas* in the National Pest Plant Accord. Raising public awareness of weed ferns in general would also be useful, as discussions with public, (including biologists and ecologists), has demonstrated that awareness of exotic ferns, let alone weed ferns, is low.

Control and progressive removal of *D. filix-mas* from indigenous remnants and adjacent areas, including suburban areas is also highly desirable. Even heavy infestations could be quickly reduced in size and the effort required for effective management significantly reduced. Such action is feasible because spore viability quickly declines, reaching zero viability beyond two years with plants taking several years to reach maturity. Most rhizomes can be easily pulled and removed for disposal and while there doesn't appear to be any literature on chemical control methods, chance experience with glyphosate (Roundup, Trounce) and triclopyr (Grazon) suggests that these chemicals may be effective. Ferns are generally considered to be susceptible to metsulfuron methyl (Escort, Muturon, Mustang), although I am unaware of any instances of this being used on *D. filix-mas*. Timing of herbicide application may be critical as in three separate instances I encountered mature *D. filix-mas* growing in the open where a brush weed canopy had recently been sprayed (triclopyr and metsulfuron methyl are commonly used in NZ for brushweeds). Persons undertaking control with herbicide would need to be well versed in distinguishing *D. filix-mas* from *Pneumatopteris pennigera*, *Hypolepis* spp., *Polystichum* spp. and *Asplenium* spp. Control operations could be used for research opportunities to investigate optimum control methods and rates of re-infestation.

Further investigations into the ecology of *D. filix-mas* and *D. affinis* in New Zealand is highly desirable to better understand the threat potential that these plants represent.

For example conditions required for sporophyte establishment, effects of propagule pressure and mechanisms for biotic resistance. Studies might also look at whether an understorey of *D. filix-mas* is more likely to be invaded by large seeded deciduous hardwoods such as sycamore (*Acer pseudoplatanus*), rowan (*Sorbus aucuparia*) or ash (*Fraxinus excelsior*) compared to a native understorey.

6 Appendices

6.1 Appendix One Male Fern gallery



Figure 6.1 Typical shaded frond of *D. filix-mas*.



Figure 6.2 A fully exposed fern from the experiment showing the dense golden scales typical of *D. filix-mas*, and the coriaceous pinnae as a response to exposure.



Figure 6.3 Underside of fertile *D. filix-mas* frond showing the kidney shaped indusia diagnostic of *Dryopteris*. In *D. affinis* the undusia edges roll right under.



Figure 6.4 *D. filix-mas* is a popular garden plant in Canterbury, in this case Rangiora.



Figure 6.5 Wild *D. filix-mas* in a native grass bed outside the School of Forestry at University of Canterbury.



Figure 6.6 *D. filix-mas* and *Dicksonia fibrosa* in the Ilam Gardens Christchurch.



Figure 6.7 *D. filix-mas* growing from under a piece of limestone masonry on concrete at University of Canterbury.



Figure 6.8 Epiphytic on a phoenix palm at Constance Bay, Timaru.



Figure 6.9 A rare occurrence on a north facing bank, but here shaded through summer by the cantilevered footpath (photo taken in winter), Timaru.



Figure 6.10 Rather robust *D. filix-mas* at Hanging Rock, South Canterbury. (Photo A. Shanks)



Figure 6.11 Regrowth on a road bank after mowing. Unusual in that the substrate is Separation Point granite (low fertility and low pH), Orinoco Valley Rd, Ngatimoti, Tasman.



Figure 6.12 Tall *D. filix-mas* on a road bank near the Conway River, which has had the brushweeds (broom and blackberry sprayed out).



Figure 6.13 Above the Rakaia River with broom and *Cotoneaster simonsii*.



Figure 6.14 Heavy growth of *D. filix-mas* at the edge of Douglas fir plantation, with a few *Polystichum vestitum* mixed in. Island Hill, Island Hills Station.



Figure 6.15 One *D. filix-mas* (left) and one *P. vestitum* in a light gap in Douglas fir. Island Hills Station.



Figure 6.16 Under sycamore (*Acer pseudoplatanus*) in the Mandamus Valley, North Canterbury.



Figure 6.17 A rare occurrence, *D. filix-mas* under beech forest (*Fuscospora solandri*), with *P. vestitum* (left). In this case a heavily grazed remnant on Melrose Station, North Canterbury.



Figure 6.18 To the left of this fertile *D. filix-mas* at Tiromoana Bush there are at least seven sterile *D. filix-mas* sporophytes.



Figure 6.19 Under the edge of a *Cupressus* plantation, *D. filix-mas* has established with *Blechnum penna-marina*, *B. fluviatile* and *P. vestitum*. Loburn, North Canterbury.



Figure 6.20 *D. filix-mas* (browsed on right) with *D. dilatata*, *B. penna-marina* and *P. vestitum* in a gap between *Pinus radiata* and Douglas fir at Island Hills Station.



Figure 6.21 *Dryopteris xtavellii*, the hybrid between *D. filix-mas* and *D. affinis*, with small plants of *D. filix-mas* on either side. Rakaia.



Figure 6.22 *D. filix-mas* in the side of a rock ravine on Melrose Station in North Canterbury. The site itself is not grazed but the slopes above are and the ravine itself probably has a history of fire and aerial fertiliser application.



Figure 6.23 Under grey scrub (*Discaria toumatou* and *Coprosma propinqua*) In the Lewis Pass.



Figure 6.24 Emerging from under rubble at the base of an alluvial terrace in the Lewis Pass.



Figure 6.25 *D. filix-mas* on limestone talus in Mead Stream, Clarence Valley.



Figure 6.26 The semi-arid Tweed basin below Lake McRae in Molesworth Station. *D. filix-mas* can be found in the incised gullies (bottom right) and along the stream under the crack willow (*Salix fragilis*).



Figure 6.27 At Hell's Gate in the Wairau Valley, Marlborough, *D. filix-mas* grows amongst the rocks and scrub on the avalanche path that occupies the middle of the photo. At the time of the photo (2014) *D. filix-mas* were not present within the beech forest.



Figure 6.28 *D. filix-mas* in an avalanche path at Hell's Gate, Marlborough



Figure 6.29 *D. filix-mas* emerging from deep within a rock pile at Hell's Gate, Marlborough.



Figure 6.30 *D. filix-mas* growing by the Wairau River, amongst speargrass (*Aciphylla aurea*) and grey scrub at Hell's Gate.

6.2 Appendix Two Field Data Form

[illegible]

6.3 Appendix Three Land Environments New Zealand attribute table for Level IV environments containing *D. filix-mas*

| LVL_4 | male fern | Ha. | Metres a.s.l. | Annual Temp | Min. Temp | Annual SolRad | Winter SolRad | OCT VPD | Water BalRatio | Water Deficit | Slope | Drain- age | Age | Chemical limitations | Acid SolP | Exchangable calcium | Induration | Particle Size |
|-------|--------------|--------|------------------|----------------|--------------|------------------|------------------|------------|-------------------|------------------|-------|---------------|-----|-------------------------|--------------|------------------------|------------|------------------|
| A6.1b | 1 | 375238 | 63 | 14.9 | 6.7 | 15.1 | 6.2 | 0.37 | 2.6 | 50.22 | 6.7 | 3 | 2 | 1 | 1.2 | 1.1 | 3.1 | 1.7 |
| A7.1a | 1 | 59018 | 113 | 14.7 | 6.4 | 15 | 6.3 | 0.37 | 2.9 | 39.47 | 1.8 | 4.8 | 2 | 1 | 3.8 | 1 | 4 | 5 |
| A7.2c | 3 | 124624 | 41 | 13.8 | 4 | 14.9 | 5.7 | 0.38 | 2.6 | 36.69 | 0.2 | 5 | 2 | 1 | 1.9 | 1.9 | 3.5 | 1.8 |
| B1.1a | 2 | 33818 | 134 | 11.9 | 1.9 | 15.3 | 4.9 | 0.44 | 2.6 | 83.69 | 7.4 | 4.9 | 2 | 1 | 1.3 | 1.3 | 2.8 | 3.1 |
| B3.1a | 11 | 55679 | 208 | 11.1 | 0.6 | 14.3 | 4.5 | 0.54 | 2 | 140.77 | 9.7 | 3.5 | 2 | 1 | 2.9 | 2.1 | 3.9 | 4.4 |
| B3.1b | 3 | 27830 | 361 | 10.5 | -0.1 | 14.4 | 4.5 | 0.55 | 2.6 | 63.9 | 11.6 | 3 | 2 | 1 | 3.2 | 2.4 | 3.9 | 4.4 |
| B3.2a | 10 | 18819 | 415 | 10.1 | -1 | 14.4 | 4.4 | 0.54 | 2.6 | 65.75 | 6.3 | 5 | 2 | 1 | 4 | 1.9 | 3.7 | 3.4 |
| B8.1b | 1 | 9484 | 184 | 11.9 | 2.3 | 14.9 | 4.8 | 0.44 | 1.7 | 212.17 | 14.6 | 4.9 | 2 | 1 | 3 | 1.5 | 3.4 | 3.4 |
| B8.1c | 1 | 40174 | 260 | 11.7 | 2.2 | 14.9 | 5.4 | 0.61 | 1.7 | 185.34 | 15.1 | 4.9 | 2 | 1 | 3 | 1.3 | 3.3 | 4.2 |
| B9.1a | 1 | 9335 | 52 | 12.5 | 2.2 | 15 | 4.9 | 0.49 | 1.4 | 274.07 | 0.9 | 4.8 | 2 | 1 | 4.2 | 2 | 3.5 | 3 |
| C2.1b | 1 | 58567 | 125 | 12.3 | 3.5 | 14 | 4.6 | 0.34 | 2.7 | 51.2 | 2.2 | 2.5 | 2 | 1 | 2 | 2 | 1 | 1 |
| C2.1d | 1 | 105540 | 222 | 11.9 | 3 | 14 | 4.6 | 0.35 | 3.1 | 30.56 | 1.9 | 5 | 2 | 1 | 2 | 2 | 1 | 1 |
| C2.1e | 1 | 54339 | 219 | 11.8 | 3.3 | 14 | 4.6 | 0.32 | 2.7 | 44.35 | 4.4 | 4 | 2 | 1 | 2 | 2 | 1 | 1 |
| C3.1b | 2 | 59118 | 94 | 12.6 | 3.4 | 14.2 | 4.7 | 0.38 | 2.3 | 98.57 | 0.6 | 5 | 2 | 1 | 2.4 | 2 | 2.3 | 1.4 |
| E1.1b | 5 | 38556 | 159 | 11.8 | 1.7 | 15.3 | 4.7 | 0.44 | 3.2 | 46.69 | 16.6 | 5 | 2 | 1 | 1.9 | 1.7 | 3.9 | 4.5 |
| E1.2a | 1 | 82119 | 626 | 9.7 | -0.4 | 14.9 | 5.4 | 0.52 | 2 | 109.81 | 22.6 | 5 | 2 | 1 | 3.1 | 1 | 3.9 | 4.1 |
| E1.2b | 1 | 13545 | 574 | 10 | 0.3 | 14.8 | 5.3 | 0.55 | 2 | 110.19 | 24.3 | 5 | 2 | 1 | 2 | 4 | 4 | 5 |
| E1.3a | 5 | 35114 | 378 | 10.7 | 1.1 | 14.6 | 4.7 | 0.57 | 2.8 | 31.26 | 23.1 | 5 | 2 | 1 | 3 | 1.2 | 3.8 | 4.1 |
| E1.3b | 2 | 30240 | 201 | 11.4 | 1.6 | 14.5 | 4.6 | 0.58 | 2.3 | 103.78 | 15.5 | 5 | 2 | 1 | 3 | 1.1 | 3.6 | 4.1 |
| E1.4c | 23 | 328673 | 749 | 8.5 | -1.7 | 14.1 | 4.6 | 0.44 | 3.1 | 12.97 | 22.7 | 5 | 2 | 1 | 3 | 1.1 | 4 | 4 |
| E1.4d | 37 | 99429 | 521 | 9.5 | -1.2 | 14.2 | 4.5 | 0.49 | 2.4 | 68.06 | 17.5 | 5 | 2 | 1 | 3 | 1.1 | 3.9 | 4 |
| E3.1a | 3 | 31551 | 565 | 8.9 | -2 | 13.3 | 4.4 | 0.38 | 2.3 | 15.68 | 10.5 | 3.9 | 2 | 1 | 3 | 2 | 2.1 | 1.1 |
| E3.2b | 4 | 37274 | 383 | 10.1 | -0.1 | 13.8 | 4.6 | 0.45 | 2.4 | 23.33 | 4.9 | 3.3 | 2 | 1 | 3.1 | 1.9 | 2.5 | 1.6 |

| LVL_4 | male fern | Ha. | Metres a.s.l. | Annual Temp | Min. Temp | Annual SolRad | Winter SolRad | OCT VPD | Water BalRatio | Water Deficit | Slope | Drain- age | Age | Chemical limitations | Acid SolP | Exchangable calcium | Induration | Particle Size |
|-------|--------------|--------|------------------|----------------|--------------|------------------|------------------|------------|-------------------|------------------|-------|---------------|-----|-------------------------|--------------|------------------------|------------|------------------|
| E4.1a | 1 | 31768 | 809 | 8.3 | -2.6 | 14.6 | 4.9 | 0.48 | 1.5 | 194.95 | 4.4 | 5 | 2 | 1 | 3.9 | 1 | 2.1 | 3 |
| E4.1b | 2 | 116251 | 672 | 8.6 | -2.5 | 14 | 4.4 | 0.45 | 2 | 90.75 | 3 | 5 | 2 | 1 | 3.9 | 1.1 | 2 | 2.9 |
| E4.2a | 4 | 112054 | 849 | 7.9 | -2.2 | 14.1 | 4.7 | 0.41 | 3.9 | 6.01 | 10.5 | 5 | 2 | 1 | 3.9 | 1 | 2.1 | 3 |
| E4.2b | 2 | 56591 | 669 | 8.8 | -1.5 | 13.9 | 4.7 | 0.45 | 2.5 | 48.9 | 8.6 | 5 | 2 | 1 | 3.9 | 1.1 | 2.1 | 2.9 |
| F1.1d | 3 | 411537 | 391 | 11.2 | 1.9 | 14.2 | 4.8 | 0.3 | 4.2 | 0.51 | 19.7 | 5 | 2 | 1 | 1.1 | 1 | 3.8 | 4.8 |
| F1.3b | 1 | 138487 | 204 | 12.2 | 3.1 | 14.4 | 4.9 | 0.36 | 3 | 18.44 | 19.6 | 4.7 | 2 | 1 | 1 | 1 | 3.5 | 5 |
| F1.4a | 1 | 112505 | 318 | 11.4 | 2.7 | 13.9 | 4.6 | 0.32 | 2.9 | 39.47 | 10 | 3.5 | 2 | 1 | 1.1 | 1 | 3.7 | 4.9 |
| F1.4b | 5 | 26709 | 138 | 12.2 | 4.7 | 14.1 | 4.4 | 0.31 | 3.3 | 42.43 | 13.9 | 3.7 | 2 | 1 | 1 | 1 | 4 | 4 |
| F1.4c | 4 | 110676 | 312 | 11.1 | 3 | 14 | 4.5 | 0.31 | 4.2 | 6.38 | 19.3 | 3.6 | 2 | 1 | 1 | 1 | 4 | 4.1 |
| F3.1a | 4 | 32452 | 120 | 11.7 | 3.4 | 13.8 | 4.5 | 0.46 | 2.2 | 175.67 | 15 | 3.6 | 2 | 1 | 3 | 2 | 2 | 1 |
| F3.1b | 3 | 22259 | 280 | 11.1 | 3.3 | 13.7 | 4.5 | 0.41 | 3.1 | 74.25 | 15.9 | 3.1 | 2 | 1 | 3 | 2 | 2 | 1 |
| F3.2a | 1 | 11166 | 199 | 11.4 | 3.5 | 13.8 | 4.6 | 0.45 | 2.3 | 147.5 | 23.1 | 5 | 2 | 1 | 4.6 | 1.7 | 3.9 | 4.8 |
| F3.3a | 4 | 15985 | 459 | 10.2 | 2.7 | 13.7 | 4.5 | 0.37 | 3.8 | 22.55 | 21.8 | 5 | 2 | 1 | 5 | 2 | 4 | 5 |
| F3.3b | 8 | 14533 | 450 | 10.2 | 2.6 | 13.7 | 4.5 | 0.39 | 3.3 | 44.62 | 19.2 | 5 | 2 | 1 | 3 | 2 | 2 | 1 |
| F5.2a | 1 | 115542 | 224 | 12.2 | 4.1 | 14.6 | 5 | 0.3 | 4.4 | 3.98 | 1.9 | 4.9 | 2 | 1 | 4.9 | 2 | 2.2 | 1.1 |
| F5.2c | 1 | 79420 | 102 | 12.8 | 4.8 | 14.5 | 4.9 | 0.35 | 2.6 | 48.34 | 3.2 | 5 | 2 | 1 | 4.7 | 1.9 | 2.1 | 1.1 |
| F6.1a | 3 | 281908 | 232 | 12.9 | 3.2 | 15.1 | 5.8 | 0.38 | 3.7 | 3.71 | 7.6 | 5 | 2 | 1 | 2 | 1.9 | 2.1 | 1.1 |
| F6.1d | 1 | 213965 | 147 | 13.1 | 3.3 | 14.6 | 5.5 | 0.33 | 2.9 | 20.21 | 4 | 5 | 2 | 1 | 2 | 2 | 2 | 1 |
| F6.1e | 2 | 60396 | 556 | 11.1 | 2.2 | 14.8 | 5.6 | 0.3 | 4.2 | 0.34 | 2.3 | 5 | 2 | 1 | 2 | 2 | 2 | 1 |
| F6.2a | 3 | 368509 | 463 | 11.5 | 2 | 14.8 | 5.7 | 0.3 | 4 | 0.73 | 25.6 | 5 | 2 | 1 | 2 | 2 | 2 | 1 |
| F7.1a | 3 | 79233 | 337 | 11.9 | 1 | 14.7 | 5.3 | 0.35 | 2.5 | 17.74 | 1.6 | 5 | 2 | 1 | 1.2 | 1 | 3.1 | 2.1 |
| F7.1b | 4 | 334446 | 521 | 11 | 1.1 | 14.6 | 5.3 | 0.31 | 3.1 | 7.43 | 6.3 | 5 | 2 | 1 | 1.2 | 1 | 3 | 2.1 |
| F7.2a | 3 | 433128 | 327 | 11.9 | 2.5 | 14.3 | 5 | 0.3 | 3.8 | 2.15 | 10.5 | 5 | 2 | 1 | 2.6 | 1.7 | 1.9 | 1 |

| LVL_4 | male fern | Ha. | Metres a.s.l. | Annual Temp | Min. Temp | Annual SolRad | Winter SolRad | OCT VPD | Water BalRatio | Water Deficit | Slope | Drain- age | Age | Chemical limitations | Acid SolP | Exchangable calcium | Induration | Particle Size |
|-------|--------------|--------|------------------|----------------|--------------|------------------|------------------|------------|-------------------|------------------|-------|---------------|-----|-------------------------|--------------|------------------------|------------|------------------|
| F7.3a | 1 | 124015 | 849 | 8.8 | 0.2 | 14.1 | 4.9 | 0.27 | 4.2 | 10.69 | 5.1 | 5 | 2 | 1 | 2 | 1 | 2.1 | 1.1 |
| H2.1c | 5 | 6925 | 398 | 11.6 | 0.6 | 14.9 | 5.5 | 0.34 | 2.9 | 13.98 | 3.7 | 4.4 | 1 | 1 | 2.8 | 2 | 1.1 | 1 |
| H2.2a | 1 | 23656 | 388 | 11.8 | 1.7 | 15 | 5.6 | 0.35 | 3.5 | 3.99 | 11.9 | 5 | 1 | 1 | 1.8 | 1.6 | 2.1 | 1.6 |
| H2.2b | 5 | 24544 | 493 | 11.2 | 1.2 | 15.1 | 5.6 | 0.34 | 4 | 1.9 | 6.1 | 5 | 1 | 1 | 4 | 1 | 4 | 3 |
| I3.3a | 1 | 9778 | 5 | 11.8 | 2.1 | 13.9 | 4.3 | 0.5 | 1.7 | 216.96 | 0.2 | 2.5 | 1 | 2 | 4 | 2 | 1 | 1 |
| I5.1a | 1 | 11773 | 24 | 13.9 | 4.1 | 14.8 | 5.9 | 0.52 | 1.9 | 145.78 | 0.2 | 3.8 | 1 | 1 | 2.8 | 2.8 | 1 | 1 |
| J1.1c | 1 | 6017 | 113 | 12 | 1.8 | 15.3 | 4.8 | 0.45 | 2.9 | 72.27 | 7.1 | 5 | 1 | 1 | 2.4 | 1.7 | 1.7 | 2 |
| J2.1b | 6 | 51032 | 34 | 11.6 | 1.3 | 13.9 | 4.2 | 0.48 | 1.7 | 212.13 | 0 | 5 | 1 | 1 | 3.9 | 2 | 3.1 | 2 |
| J2.1d | 2 | 3205 | 26 | 12.1 | 3.2 | 13.9 | 4.6 | 0.49 | 1.9 | 208.63 | 3.9 | 5 | 1 | 1 | 3.1 | 2 | 2.3 | 1.4 |
| J2.2a | 1 | 10138 | 579 | 9.1 | -2 | 14.2 | 4.7 | 0.49 | 2.1 | 93.73 | 0.7 | 5 | 1 | 1 | 4 | 2 | 4 | 3 |
| J2.2b | 1 | 22721 | 185 | 10.8 | 0.1 | 14 | 4.5 | 0.48 | 1.8 | 128.2 | 0.1 | 5 | 1 | 1 | 4 | 2 | 3.9 | 2.9 |
| J3.1a | 1 | 6995 | 93 | 12.2 | 3.6 | 14.7 | 4.8 | 0.62 | 2.1 | 117.94 | 2.7 | 4.9 | 2 | 1 | 3.8 | 1.9 | 3.9 | 3.2 |
| J4.2a | 2 | 7296 | 40 | 13.2 | 5.3 | 14.5 | 4.9 | 0.37 | 2.4 | 70.54 | 1.9 | 5 | 1 | 1 | 2.4 | 1.9 | 3.6 | 1.9 |
| J4.2b | 2 | 17934 | 19 | 13 | 4 | 14.4 | 4.7 | 0.38 | 2 | 118.47 | 0.6 | 5 | 1 | 1 | 2.8 | 1.9 | 3.9 | 2 |
| K1.1a | 3 | 13552 | 683 | 8.6 | -1.7 | 13.9 | 4.6 | 0.42 | 6.1 | 0.13 | 4.4 | 5 | 1 | 1 | 4 | 2 | 4 | 3 |
| K1.1b | 5 | 33251 | 571 | 9.2 | -1.2 | 13.9 | 4.8 | 0.46 | 3 | 17.05 | 3.7 | 5 | 1 | 1 | 4 | 2 | 4 | 3 |
| K1.1d | 1 | 6954 | 958 | 7.4 | -3.2 | 14.5 | 4.8 | 0.39 | 3.3 | 14.93 | 5.3 | 5 | 1 | 1 | 4 | 2 | 4 | 3 |
| L1.1d | 3 | 24843 | 22 | 10.1 | 1.5 | 12.3 | 3.1 | 0.32 | 3.2 | 12.48 | 0.4 | 5 | 1 | 1 | 3.5 | 2 | 2.9 | 1.5 |
| L1.2a | 1 | 16156 | 148 | 10.5 | -0.7 | 13.3 | 4.1 | 0.4 | 1.8 | 69.05 | 0.2 | 5 | 1 | 1 | 4 | 2 | 4 | 3 |
| L2.2b | 1 | 1681 | 11 | 10.3 | 0.9 | 12.3 | 3.5 | 0.4 | 1.9 | 99.07 | 1 | 2 | 1 | 2 | 4 | 2 | 1 | 1 |
| L3.1a | 1 | 55191 | 36 | 10 | 1.5 | 12.3 | 3.1 | 0.32 | 3.3 | 14.24 | 0.2 | 1 | 2 | 1 | 1.4 | 2 | 1.2 | 1.1 |
| L3.2a | 1 | 35386 | 73 | 9.6 | 1.4 | 12.3 | 3 | 0.31 | 4.2 | 4.76 | 2 | 2 | 2 | 1 | 1.8 | 1 | 2.8 | 3.4 |
| L4.1a | 4 | 318116 | 152 | 9.7 | 0.4 | 12.4 | 3.3 | 0.36 | 2.4 | 49.52 | 4.1 | 3 | 2 | 1 | 3.1 | 2 | 2 | 1.1 |

| LVL_4 | male fern | Ha. | Metres a.s.l. | Annual Temp | Min. Temp | Annual SolRad | Winter SolRad | OCT VPD | Water BalRatio | Water Deficit | Slope | Drain- age | Age | Chemical limitations | Acid SolP | Exchangable calcium | Induration | Particle Size |
|-------|--------------|--------|------------------|----------------|--------------|------------------|------------------|------------|-------------------|------------------|-------|---------------|-----|-------------------------|--------------|------------------------|------------|------------------|
| M2.1a | 1 | 45005 | 87 | 11.3 | 1.4 | 13 | 3.9 | 0.26 | 8.7 | 0 | 1.3 | 5 | 1 | 1 | 3.9 | 1 | 2 | 3 |
| M2.2a | 1 | 6173 | 378 | 10.1 | -0.9 | 13.9 | 4.2 | 0.34 | 5 | 0.02 | 1.6 | 5 | 1 | 1 | 4 | 1.3 | 2.6 | 3 |
| N1.1a | 4 | 179949 | 89 | 11.3 | 0.5 | 14 | 4.3 | 0.48 | 1.7 | 185.24 | 0 | 4.6 | 2 | 1 | 3.9 | 2 | 3.8 | 2.8 |
| N1.1b | 1 | 31062 | 172 | 11.2 | 0.1 | 14.3 | 4.5 | 0.55 | 1.6 | 195.74 | 1.8 | 4.9 | 2 | 1 | 3.1 | 2 | 2.4 | 2.6 |
| N1.2a | 3 | 64536 | 140 | 11.4 | 0.9 | 14.2 | 4.5 | 0.54 | 1.8 | 173.15 | 3.6 | 2.9 | 2 | 1 | 3.1 | 2 | 2 | 1 |
| N1.2b | 2 | 46958 | 108 | 11 | 0.2 | 13.9 | 4.4 | 0.47 | 1.7 | 138.81 | 0.1 | 3 | 2 | 1 | 3.7 | 2 | 2.2 | 1.2 |
| N1.2c | 13 | 65751 | 22 | 11.6 | 1.1 | 13.8 | 4.2 | 0.47 | 1.7 | 203.4 | 0.1 | 1.9 | 2 | 1 | 3.7 | 2 | 2 | 1 |
| N2.1a | 4 | 198798 | 195 | 10.8 | 0 | 13.9 | 4.5 | 0.47 | 1.9 | 97.39 | 0.1 | 4.8 | 2 | 1 | 4 | 2 | 4 | 3 |
| N2.1b | 1 | 41382 | 264 | 10.7 | 0.5 | 13.9 | 4.7 | 0.47 | 2 | 84.2 | 0.3 | 4.9 | 2 | 1 | 3 | 2 | 2 | 1 |
| N2.1c | 13 | 55956 | 397 | 10.1 | 0.1 | 13.8 | 4.8 | 0.46 | 2.4 | 13.3 | 1.2 | 5 | 2 | 1 | 3.9 | 1.9 | 3.8 | 2.8 |
| N2.1d | 3 | 70959 | 279 | 10 | -1.1 | 13.4 | 4.3 | 0.41 | 2 | 24.53 | 0.5 | 4.9 | 2 | 1 | 4 | 2 | 4 | 3 |
| N2.2a | 1 | 68670 | 58 | 10.7 | 0.3 | 12.9 | 4.1 | 0.4 | 1.3 | 166.79 | 0.2 | 4.2 | 2 | 1 | 3.9 | 2 | 3.7 | 2.8 |
| N3.1a | 14 | 120224 | 289 | 9.8 | -1.4 | 13.1 | 4.2 | 0.4 | 1.8 | 72.78 | 5.6 | 3 | 2 | 1 | 3.1 | 2 | 2 | 1 |
| N3.1b | 3 | 101515 | 70 | 10.7 | 0.4 | 13 | 4.2 | 0.4 | 1.3 | 151.79 | 1 | 3 | 2 | 1 | 3.2 | 2 | 2 | 1 |
| N3.1d | 3 | 62505 | 514 | 8.6 | -2.6 | 13.2 | 4 | 0.39 | 1.6 | 112.73 | 4.6 | 4 | 2 | 1 | 3.3 | 2 | 3.1 | 2.7 |
| N3.3a | 2 | 101614 | 234 | 9.7 | -0.6 | 12.8 | 3.9 | 0.39 | 1.5 | 129.35 | 5.6 | 5 | 2 | 1 | 2.8 | 2.2 | 3.2 | 2.8 |
| N4.1d | 2 | 46758 | 487 | 9.1 | -2.6 | 13.9 | 3.7 | 0.45 | 1.7 | 175.53 | 16 | 4.1 | 2 | 1 | 3 | 2 | 3.7 | 3.8 |
| N5.1c | 2 | 37340 | 363 | 9.9 | -1.9 | 14 | 3.7 | 0.47 | 1.6 | 202.34 | 2.9 | 4.3 | 2 | 1 | 3 | 2 | 2 | 2.9 |
| O1.1a | 1 | 97186 | 216 | 11.1 | 1.7 | 13.8 | 4.3 | 0.25 | 7.1 | 0.01 | 12.3 | 5 | 2 | 1 | 2.6 | 1 | 2.5 | 4.5 |
| O1.4b | 1 | 112501 | 218 | 10.7 | 0.8 | 13.1 | 3.9 | 0.25 | 8.1 | 0 | 11.3 | 5 | 2 | 1 | 1.3 | 1 | 2.2 | 3.1 |
| P1.2a | 5 | 228726 | 1228 | 6.2 | -3.6 | 14.6 | 4.9 | 0.36 | 3.6 | 5.99 | 27.9 | 5 | 2 | 1 | 3 | 1 | 4 | 4 |
| P1.2d | 4 | 524794 | 1208 | 6.1 | -2.9 | 13.8 | 4.7 | 0.33 | 5.1 | 0.63 | 27.8 | 5 | 2 | 1 | 3 | 1 | 4 | 4 |
| P2.1b | 2 | 53694 | 1508 | 4.6 | -4.5 | 14.4 | 4.8 | 0.23 | 5.8 | 0.02 | 29 | 3 | 2 | 1 | 3 | 1 | 4 | 4 |

| LVL_4 | male fern | Ha. | Metres a.s.l. | Annual Temp | Min. Temp | Annual SolRad | Winter SolRad | OCT VPD | Water BalRatio | Water Deficit | Slope | Drain- age | Age | Chemical limitations | Acid SolP | Exchangable calcium | Induration | Particle Size |
|--------|--------------|--------|------------------|----------------|--------------|------------------|------------------|------------|-------------------|------------------|-------|---------------|-----|-------------------------|--------------|------------------------|------------|------------------|
| P5.1b | 1 | 57066 | 625 | 9 | -1.7 | 14 | 4.2 | 0.26 | 5.4 | 0 | 22.9 | 5 | 2 | 1 | 3.4 | 2.1 | 4 | 4.8 |
| P5.2a | 3 | 108935 | 447 | 9.8 | -0.8 | 14 | 4.2 | 0.31 | 5.3 | 0.04 | 13.5 | 5 | 2 | 1 | 2.8 | 1.1 | 2.1 | 2.7 |
| Q1.1d | 3 | 248415 | 962 | 6.6 | -2.5 | 13.1 | 3.9 | 0.29 | 3.4 | 0.9 | 21.6 | 5 | 2 | 1 | 3 | 1 | 3.9 | 4 |
| Q2.1a | 1 | 229284 | 636 | 8.4 | -1.9 | 13.1 | 4 | 0.35 | 2.5 | 16.4 | 18 | 5 | 2 | 1 | 3 | 1.1 | 4 | 4 |
| Q2.1c | 4 | 86229 | 443 | 8.9 | -1.5 | 12.9 | 4 | 0.36 | 1.8 | 72.27 | 16.4 | 5 | 2 | 1 | 3.1 | 1.2 | 3.9 | 4 |
| Q2.2a | 4 | 214800 | 762 | 7.6 | -3.2 | 13.7 | 3.7 | 0.38 | 2.5 | 74.02 | 21.1 | 4 | 2 | 1 | 3 | 2 | 4 | 4 |
| Q2.2b | 5 | 25048 | 428 | 9.6 | -0.9 | 13.9 | 3.8 | 0.42 | 2.7 | 70.2 | 13.6 | 4.2 | 2 | 1 | 3 | 2 | 2.6 | 3.1 |
| Q4.2b | 1 | 117849 | 168 | 9.4 | 1.1 | 12.2 | 3.1 | 0.3 | 3.6 | 7.84 | 4.3 | 4.8 | 2 | 1 | 3.8 | 2 | 2 | 1 |
| Q4.2c | 3 | 153183 | 54 | 9.9 | 1 | 12.4 | 3.1 | 0.33 | 3.2 | 19.44 | 0.3 | 4.2 | 2 | 1 | 3.5 | 2.2 | 2.1 | 1.3 |
| Q4.3a | 1 | 232975 | 399 | 8.6 | -0.4 | 12.6 | 3.5 | 0.35 | 2.6 | 28.66 | 12.4 | 4 | 2 | 1 | 3 | 1.9 | 3.9 | 4 |
| Q4.3c | 1 | 42166 | 119 | 9.7 | 0.9 | 12.2 | 3.3 | 0.34 | 2.3 | 68.4 | 9.2 | 4 | 2 | 1 | 2 | 1.1 | 4 | 4 |
| Q4.3d | 9 | 21364 | 177 | 9.8 | 2.6 | 12.3 | 3.8 | 0.37 | 2.4 | 45.45 | 12.9 | 5 | 2 | 1 | 3.4 | 1.4 | 3.8 | 4.9 |
| R1.1a | 1 | 200298 | 1111 | 6.4 | -2.9 | 13.5 | 4.2 | 0.23 | 9 | 0 | 31.3 | 4.9 | 2 | 1 | 3 | 1.5 | 4 | 4 |
| Min | | 1681 | 5 | 4.6 | -4.5 | 12.2 | 3 | 0.23 | 1.3 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Max | | 524794 | 1508 | 14.9 | 6.7 | 15.3 | 6.3 | 0.62 | 9 | 274.07 | 31.3 | 5 | 2 | 2 | 5 | 4 | 4 | 5 |
| Median | | | 260 | 10.7 | 0.9 | 14.0 | 4.6 | 0.39 | 2.6 | 46.7 | 5.6 | 5.0 | 2.0 | 1.0 | 3.0 | 1.9 | 3.1 | 2.9 |
| Mean | | | 345 | 10.5 | 0.8 | 14.0 | 4.5 | 0.40 | 3.0 | 68.1 | 8.8 | 4.4 | 1.8 | 1.0 | 3.0 | 1.7 | 2.9 | 2.7 |

6.4 Appendix Four Species list

To make checking codes against the list easier the following species list, recorded during the field survey, is arranged alphabetically by the species codes used in the ordination and displayed on the ordination diagrams. This is a departure from the normal practice of dividing the list into botanical classes (gymnosperms, ferns, etc.).

| Code in ordination graphs | Scientific Name | Common name | Class and Comments |
|---------------------------|-----------------------------------|----------------------|--------------------|
| Acaena | <i>Acaena</i> species | bidibidi/piripiri | Dicot |
| ACEpse | <i>Acer pseudoplatanus</i> | sycamore | Dicot |
| ACHmil | <i>Achillea millefolium</i> | yarrow | Composite |
| ADIcun | <i>Adiantum cunninghamii</i> | maidenhair fern | Fern |
| AGRcap | <i>Agrostis capillaris</i> | browntop | Grass |
| ANabel | <i>Anaphalioides bellidioides</i> | everlasting daisy | Composite |
| HELfil | <i>Heilichrysus filicaule</i> | everlasting daisy | Composite |
| ANIaro | <i>Anisotome aromatica</i> | | Dicot |
| ANIfil | <i>Anisotome filifolia</i> | | Dicot |
| ANTcau | <i>Anthriscus caucalis</i> | beaked parsley | Dicot |
| ANTodo | <i>Anthoxanthum odoratum</i> | sweet vernal | Grass |
| ARHela | <i>Arrhenatherum elatius</i> s.l. | tall oat grass | Grass |
| ARIfru | <i>Aristotelia fruticosa</i> | mountain wineberry | Dicot |
| ARIserr | <i>Aristotelia serrata</i> | wineberry | Dicot |
| ARTcan | <i>Arthropodium candidum</i> | | Monocot |
| ASPapp | <i>Asplenium appendiculatum</i> | ground spleenwort | Fern |
| ASPbul | <i>Asplenium bulbiferum</i> | hen and chicken fern | Fern |
| ASPflab | <i>Asplenium flabellifolium</i> | necklace fern | Fern |
| ASPflac | <i>Asplenium flaccidum</i> | bootlace fern | Fern |
| ASPgra | <i>Asplenium gracillimum</i> | hen and chicken fern | Fern |
| ASPPhoo | <i>Asplenium bookerianum</i> | | Fern |
| ASPla | <i>Asplenium lyallii</i> | | Fern |
| ASPrich | <i>Asplenium richardii</i> | | Fern |
| ASPtri | <i>Asplenium trichomanes</i> | | Fern |
| ASTfra | <i>Astelia fragrans</i> | | Monocot |
| BELper | <i>Bellis perennis</i> | daisy | Composite |
| BLEcha | <i>Blechnum chambersii</i> | | Fern |
| BLEcol | <i>Blechnum colensoi</i> | | Fern |
| BLEdis | <i>Blechnum discolor</i> | crown fern | Fern |
| BLEflu | <i>Blechnum fluviale</i> | kiwikipi | Fern |
| BLEmin | <i>Blechnum minus</i> | swamp kiokio | Fern |
| BLEnov | <i>Blechnum novae-zealandiae</i> | kiokio | Fern |
| BLEpen | <i>Blechnum penna-marina</i> | | Fern |
| BLEpro | <i>Blechnum procerum</i> | small kiokio | Fern |
| BLEvul | <i>Blechnum vulcanicum</i> | korokio | Fern |
| Botrychium | <i>Botrychium</i> spp. | parsley fern | Fern |
| Bromus | <i>Bromus</i> spp. | various bromes | Grass |
| Calystegia | <i>Calystegia tuguriorum</i> | bindweed | Dicot |
| CARaus | <i>Carmichaelia australis</i> | common broom | Dicot |
| CARbrev | <i>Carex breviculmis</i> | | Sedge |
| CARcor | <i>Carex coriacea</i> | rautahi, cutty grass | Sedge |
| CARdeb | <i>Cardamine debilis</i> agg. | peppercress | Dicot |

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|-------------|--------------------------------|----------------------------|---|
| Carex | <i>Carex</i> species | sedges | Sedge |
| CARfor | <i>Carex forsteri</i> | Forster's sedge | Sedge |
| CARflag | <i>Carex flagellifera</i> | trip me up | Sedge |
| CARsec | <i>Carex secta</i> | purei | Sedge |
| CARser | <i>Carpodetus serratus</i> | marble-leaf | Dicot |
| CARsol | <i>Carex solandri</i> | forest sedge | Sedge |
| CARtes | <i>Carex testacea</i> | speckled sedge | Sedge |
| CASlep | <i>Cassinia leptophylla</i> | tawhini | Composite |
| CELspe | <i>Celmisia spectabilis</i> | a mountain daisy | Composite |
| CERfon | <i>Cerastium fontanum</i> | mouse-ear chickweed | Dicot |
| CERglo | <i>Cerastium glomeratum</i> | annual mouse-ear chickweed | Dicot |
| Chionochloa | <i>Chionochloa</i> spp. | snowgrasses | Grass |
| CIRarv | <i>Cirsium arvense</i> | Californian thistle | Composite |
| CIRvul | <i>Cirsium vulgare</i> | Scotch thistle | Composite |
| CLEafo | <i>Clematis afoliata</i> | leafless clematis | dicot |
| CLEfor | <i>Clematis forsteri</i> | native clematis | Dicot |
| CLEmar | <i>Clematis marata</i> | native clematis | Dicot |
| Clematis | <i>Clematis</i> sp. | native clematis | Seedlings possibly <i>C. foetida</i> . Dicot |
| CLEpan | <i>Clematis paniculata</i> | puawhananga | Dicot |
| CONmac | <i>Conium maculatum</i> | hemlock | Dicot |
| Conyza | <i>Conyza</i> spp. | fleabane | Composite |
| COPcil | <i>Coprosma ciliata</i> | | Dicot |
| COPcra | <i>Coprosma crassifolia</i> | | Dicot |
| COPdep | <i>Coprosma depressa</i> | | Dicot |
| COPlin | <i>Coprosma linariifolia</i> | yellow wood | Dicot |
| COPluc | <i>Coprosma lucida</i> | shining karamu | Dicot |
| COPmic | <i>Coprosma microphylla</i> | | Dicot |
| COPpro | <i>Coprosma propinqua</i> | mingimangi | Dicot |
| COPrha | <i>Coprosma rhamnoides</i> | | Dicot |
| COPrig | <i>Coprosma rigida</i> | | Dicot |
| COProb | <i>Coprosma robusta</i> | karamu | Dicot |
| COProt | <i>Coprosma rotundifolia</i> | | Dicot |
| COPtay | <i>Coprosma dumosa</i> | | Dicot |
| COPxcun | <i>Coprosma x cunninghamii</i> | | Dicot |
| CORaus | <i>Cordyline australis</i> | ti, cabbage tree | Monocot |
| CORcot | <i>Corokia cotoneaster</i> | korokio | Dicot |
| CORIarb | <i>Coriaria arborescens</i> | tree tutu | Dicot |
| CORric | <i>Cortaderia richardii</i> | toetoe | Dicot |
| CORSar | <i>Coriaria sarmentosa</i> | shrub tutu | Dicot |
| CORtri | <i>Corybas trilobus</i> | spider orchid | Orchid |
| Cotoneaster | <i>Cotoneaster</i> spp. | cotoneaster | Dicot |
| CRAMon | <i>Crataegus Monocotgyna</i> | hawthorn | Dicot |
| CREcap | <i>Crepis capillaris</i> | hawk's beard | Composite |
| CYAcot | <i>Cyathea colensoi</i> | mountain tree fern | fern |
| CYAsmi | <i>Cyathea smithii</i> | katote, soft tree fern | Fern |

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|-------------|---|--|---|
| CYStas | <i>Cystopteris tasmanica</i> | bladder fern | Fern |
| CYTSCO | <i>Cytisus scoparius</i> | Scottish broom | Dicot |
| DACdac | <i>Dacrycarpus dacrydioides</i> | kahikatea | Gymnosperm |
| DACglo | <i>Dactylus glomeratus</i> | cock's foot | Grass |
| DIAnig | <i>Dianella nigra</i> | NZ blue berry | Monocot |
| Dichelachne | <i>Dichelachne</i> spp. | plume grass | Grass |
| DICrep | <i>Dichondra repens</i> | Mercury Bay weed | dicot |
| DIGpur | <i>Digitalis purpurea</i> | foxglove | Dicot |
| DISTou | <i>Discaria toumatou</i> | matagouri | Dicot |
| DRAlon | <i>Dracophyllum longifolium</i> | turpentine scrub | Dicot |
| DRYaff | <i>Dryopteris affinis</i> | scaly male fern | Fern |
| DRYdil | <i>Dryopteris dilatata</i> | broad buckler fern | Fern |
| DRYfil | <i>Dryopteris filix-mas</i> | male fern | Fern |
| DRYxtav | <i>Dryopteris xtavellii</i> | <i>D. affinis</i> x <i>D. filix-mas</i> . Fern | |
| ECHova | <i>Echinopogon ovatus</i> | hedgehog grass | Grass |
| EINtri | <i>Einadia triandra</i> | pigweed | Dicot |
| ELAhoo | <i>Elaeocarpus bookerianus</i> | pokaka | Dicot |
| Elymus | <i>Elymus</i> spp. | wheat grass | Grass |
| EPIals | <i>Epilobium alsinoides</i> | willowherb | Dicot |
| EPIinsul | <i>Epilobium insulare</i> | willowherb | Dicot |
| Epilobium | <i>Epilobium</i> spp. | willowherb | Dicot |
| EPIner | <i>Epilobium nerteroides</i> | willowherb | Dicot |
| EPIpictum | <i>Epilobium pictum</i> | willowherb | Dicot |
| EPIrot | <i>Epilobium rotundifolium</i> | willowherb | Dicot |
| Erechtites | <i>Senecio</i> spp. | fireweeds | Formerly <i>Erechtites</i> . Composite |
| EUOeur | <i>Euonymus europaeus</i> | spindle berry | Dicot |
| FESnz | <i>Festuca novae-zeelandiae</i> | hard tussock | Grass |
| FESrub | <i>Festuca rubra</i> | Chewing's fescue | Grass |
| FRAGAvesca | <i>Fragaria vesca</i> | wild strawberry | Dicot |
| FUCexc | <i>Fuchsia excorticata</i> | tree fuchsia | Dicot |
| FUCper | <i>Fuchsia perscandens</i> | scrambling fuchsia | Dicot |
| Fumaria | <i>Fumaria</i> spp. | fumitory | Dicot |
| GALapa | <i>Galium aparine</i> | cleavers | Dicot |
| GALper | <i>Galium perpusillum</i> | native bedstraw | Dicot |
| GALpro | <i>Galium propinquum</i> | native bedstraw | Dicot |
| Gastrodia | <i>Gastrodia</i> sp. | potato orchid | Orchid |
| GAUant | <i>Gaultheria antipoda</i> | bush snow berry | Dicot |
| GAUnov | <i>Gaultheria depressa</i> var. <i>novae-zeelandiae</i> | snow berry | Dicot |
| Geranium | <i>Geranium</i> spp. | | Dicot |
| GNAaud | <i>Euchiton audax</i> | | Composite |
| Gnaphalium | <i>Euchiton</i> spp. | cudweed | Composite. <i>Euchiton</i> is a recent name change for native <i>Gnaphalium</i> . |
| Grammitis | <i>Grammitis</i> sp. | strap fern | Fern |
| GRIlit | <i>Griselinia littoralis</i> | broadleaf | Dicot |
| HALere | <i>Haloragis erecta</i> | | Dicot |
| HEBbra | <i>Hebe brachysiphon</i> | | Dicot |

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|----------|--|------------------------|-----------|
| HEBlei | <i>Hebe leiophylla</i> | | Dicot |
| HEBsal | <i>Hebe salicifolia</i> | koromiko | Dicot |
| HEBtra | <i>Hebe traversii</i> | | Dicot |
| HEBven | <i>Hebe venustula</i> | | Dicot |
| HELLan | <i>Helichrysum lanceolatum</i> | | Composite |
| HIEcae | <i>Hieracium caespitosum</i> | field hawkweed | Composite |
| HIElep | <i>Hieracium lepidulum</i> | tussock hawkweed | Composite |
| HIEpil | <i>Hieracium pilosella</i> | mouse-ear hawkweed | Composite |
| HIEred | <i>Hierochloa redolens</i> | holy grass/karetu | Grass |
| HISinc | <i>Histiopteris incisa</i> | water fern | Fern |
| HOHang | <i>Hoheria angustifolia</i> | narrow leaved lacebark | Dicot |
| HOLlan | <i>Holcus lanatus</i> | Yorkshire fog | Grass |
| HYDmos | <i>Hydrocotyle moschata</i> | hairy pennywort | Dicot |
| HYDpen | <i>Hydrocotyle heteromeria</i> | pennywort | Dicot |
| HYPamb | <i>Hypolepis ambigua</i> | | Fern |
| HYPEandr | <i>Hypericum androsaemum</i> | tutsan | Dicot |
| HYPlac | <i>Hypolepis lactea</i> | | Fern |
| HYPmil | <i>Hypolepis millefolium</i> | thousand leaf fern | Fern |
| HYPrad | <i>Hypochaeris radicata</i> | catsear | Monocot |
| HYPruf | <i>Hypolepis rufobarbata</i> | | Fern |
| Juncus | <i>Juncus</i> spp. | rushes | Rush |
| JUNeff | <i>Juncus effuses</i> | | Rush |
| KUNeri | <i>Kunzea ericoides</i> | kanuka | Dicot |
| LAGstr | <i>Lagenophora strangulata</i> | parani | Composite |
| LAPcom | <i>Lapsana communis</i> | nipple wort | Composite |
| LEPhym | <i>Leptopteris hymenophylloides</i> | crepe fern | Fern |
| Lepidium | <i>Lepidium</i> spp. | scurvy grass | Dicot |
| LEPnz | <i>Leptolepia novae-zelandiae</i> | lace fern | Fern |
| LEPsko | <i>Leptospermum scoparium</i> | manuka | Dicot |
| LEPsqu | <i>Leptinella squalida</i> | button daisy | Composite |
| LEUfas | <i>Leucopogon fasciculatus</i> | mingimingi | Dicot |
| LEUjun | <i>Leucopogon juniperina</i> | prickly mingimingi | Dicot |
| LEYfor | <i>Leycesteria formosa</i> | himalayan honeysuckle | Dicot |
| Libertia | <i>Libertia</i> sp. (<i>L. ixiooides</i> ?) | native iris | Monocot |
| Lolium | <i>Lolium</i> spp. | rye grass | Grass |
| LOTped | <i>Lotus pedunculatus</i> | trefoil | Dicot |
| Luzula | <i>Luzula</i> spp. | woodrush | Rush |
| LYCfas | <i>Lycopodium fastigiatum</i> | clubmoss | Fern ally |
| LYCvar | <i>Lycopodium varium</i> | clubmoss | Fern ally |
| LYCvol | <i>Lycopodium volubile</i> | waewaekoukou | Fern ally |
| MACexc | <i>Macropiper excelsum</i> | kawakawa | Dicot |
| MELalp | <i>Meliclytus alpinus</i> | porcupine shrub | Dicot |
| MELram | <i>Meliclytus ramiflorus</i> | mahoe | Dicot |
| MELsim | <i>Melicope simplex</i> | poataniwha | Dicot |
| METdif | <i>Metrosideros diffusa</i> | climbing rata | Dicot |
| MICave | <i>Microlaena avenacea</i> | bush rice grass | Grass |
| MICpus | <i>Microsorium pustulatum</i> | hounds tongue | Fern |

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|-------------|------------------------------------|------------------------|--|
| MICsti | <i>Microlaena stipoides</i> | slender rice grass | Grass |
| MUEaus | <i>Muehlenbeckia australis</i> | pohuehue | Dicot |
| MUEaxi | <i>Muehlenbeckia axillaris</i> | creeping pohuehue | Dicot |
| MUEcom | <i>Muehlenbeckia Compositelixa</i> | pohue | Dicot |
| MYCmur | <i>Mycelis muralis</i> | wall lettuce | Composite |
| MYOlac | <i>Myoporum laetum</i> | ngaio | Dicot |
| MYRaus | <i>Myrsine australis</i> | mapou | Dicot |
| MYRdiv | <i>Myrsine divaricata</i> | weeping mapou | Dicot |
| NAStri | <i>Nassella trichotoma</i> | nassella tussock | Grass |
| NEOcol | <i>Pseudopanax colensoi</i> | mountain five finger | Dicot |
| NEOped | <i>Neomyrtus pedunculatus</i> | rohutu | Dicot |
| NERdep | <i>Nertera depressa</i> | beadplant | Dicot |
| NERdic | <i>Nertera villosa</i> | forest nertera | Dicot |
| NOTfus | <i>Fuscospora fusca</i> | red beech | Dicot |
| NOTsol | <i>Fuscospora solandri</i> | black beech | Dicot |
| OLEarb | <i>Olearia arborescens</i> | glossy tree daisy | Composite |
| OLEavi | <i>Olearia avicennifolia</i> | tree daisy | Composite |
| OLEcym | <i>Olearia cymbifolia</i> | | Composite |
| OLEpan | <i>Olearia paniculata</i> | golden akeake | Composite |
| Oreomyrrhis | <i>Chaerophyllum</i> spp. | | Dicot |
| Orobanche | <i>Orobanche minor</i> | broomrape | Dicot |
| OXAmag | <i>Oxalis magellanica</i> | native oxalis | Dicot |
| PARcap | <i>Parsonsia capsularis</i> | native jasmine | Dicot |
| PARdeb | <i>Parietaria debilis</i> | NZ pellitory | Dicot |
| PARhet | <i>Parsonsia heterophylla</i> | native jasmine | Dicot |
| PELrot | <i>Pelaea rotundifolia</i> | button fern | Fern |
| PHOcoo | <i>Phormium cookianum</i> | wharariki flax | Monocot |
| PINmur | <i>Pinus muricata</i> | Bishop pine | Gymnosperm |
| PINrad | <i>Pinus radiata</i> | radiata | Gymnosperm |
| Pinus | <i>Pinus</i> spp. | exotic pines | Gymnosperm |
| PITdiv | <i>Pittosporum divaricatum</i> | | Dicot |
| PITeug | <i>Pittosporum eugenoides</i> | tarata, lemonwood | Dicot |
| PITten | <i>Pittosporum tenuifolium</i> | kohuhu | Dicot |
| PLAlan | <i>Plantago lanceolata</i> | narrow leaved plantain | Dicot |
| PNEpen | <i>Pneumatopteris pennigera</i> | gully fern | Fern |
| POAcit | <i>Poa cita</i> | silver tussock | Grass |
| POAcol | <i>Poa colensoi</i> | blue tussock | Grass |
| POAimb | <i>Poa imbecilla</i> | | Grass |
| POAprat | <i>Poa pratensis</i> | Kentucky blue-grass | Grass |
| PODcun | <i>Podocarpus cunninghamii</i> | mountain totara | Gymnosperm |
| PODtot | <i>Podocarpus totara</i> | totara | Gymnosperm |
| POLric | <i>Polystichum richardii</i> s.l. | shield fern | Fern. <i>P. oculatum</i> + <i>P. neozelandicum</i> |
| POLves | <i>Polystichum vestitum</i> | prickly shield fern | Fern |
| POLvul | <i>Polypodium vulgare</i> | common polypody | Fern |
| PRAang | <i>Lobelia angulata</i> | pratia | Dicot |
| PRUlau | <i>Prunus laurocerasus</i> | cherry laurel | Dicot |
| Prunus | <i>Prunus</i> spp. | plum & cherry | Dicot |

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|--------------|-------------------------------------|------------------------|------------|
| PRUvul | <i>Prunella vulgaris</i> | selfheal | Dicot |
| PSEarb | <i>Pseudopanax arboreus</i> | five finger | Dicot |
| PSEcol | <i>Pseudowintera colorata</i> | horopito pepperwood | Dicot |
| PSEcra | <i>Pseudopanax crassifolia</i> | lancewood | Dicot |
| PSEfer | <i>Pseudopanax ferox</i> | fierce lancewood | Dicot |
| PSElut | <i>Pseudognaphalium luteo-album</i> | Jersey cudweed | Composite |
| PSEmen | <i>Pseudotsuga menziesii</i> | Douglas fir | Gymnosperm |
| PTEalo | <i>Pterostylis alobula</i> | greenhood orchid | Orchid |
| PTEesc | <i>Pteridium esculentum</i> | bracken | Fern |
| RANfol | <i>Ranunculus foliosus</i> | a native buttercup | dicot |
| RANref | <i>Ranunculus reflexus</i> | a forest buttercup | Dicot |
| RANrep | <i>Ranunculus repens</i> | buttercup | Dicot |
| RAUano | <i>Raukawa anomalous</i> | | Dicot |
| RIBuva | <i>Ribes uva-crispa</i> | goose berry | Dicot |
| RIPsca | <i>Ripogonum scandens</i> | supple jack | Monocot |
| ROSRub | <i>Rosa rubiginosa</i> | sweet briar | Dicot |
| RUBcis | <i>Rubus cissoides</i> | bush lawyer | Dicot |
| RUBfru | <i>Rubus fruticosus</i> agg. | blackberry/bramble | Dicot |
| RUBsch | <i>Rubus schmidelioides</i> | bush lawyer | Dicot |
| RUBsqu | <i>Rubus squarrosus</i> | leafless bush lawyer | Dicot |
| RUMace | <i>Rumex acetosella</i> | sheep's sorrel | Dicot |
| Rytidosperma | <i>Rytidosperma</i> spp. | rytidosperra | Grass |
| SALcin | <i>Salix cinerea</i> | grey/pussy willow | Dicot |
| SAMnig | <i>Sambucus nigra</i> | elder | Dicot |
| SCAgen | <i>Scandia geniculata</i> | scandia | Dicot |
| SCHdig | <i>Schefflera digitata</i> | pate | Dicot |
| SENjac | <i>Senecio jacobaea</i> | ragwort | Composite |
| SENVul | <i>Senecio vulgaris</i> | groundsel | Composite |
| SENwai | <i>Senecio wairauensis</i> | a native groundsel | Composite |
| Solanum | <i>Solanum</i> spp. (herbs) | nightshades | dicot |
| SOLLac | <i>Solanum laciniatum</i> | poroporo | Dicot |
| SOLnig | <i>Solanum nigrum</i> | black nightshade | Dicot |
| SONole | <i>Sonchus oleraceus</i> | sow thistle | Composite |
| SOPmic | <i>Sophora microphylla</i> | kowhai | Dicot |
| STEdec | <i>Stellaria decipiens</i> | a native chickweed | Dicot |
| STEgra | <i>Stellaria graminea</i> | stitchwort | Dicot |
| STEmed | <i>Stellaria media</i> | chickweed | Dicot |
| TARoff | <i>Taraxacum officinalis</i> | dandelion | Composite |
| Thelymitra | <i>Thelymitra</i> spp. | sun orchid | Orchid |
| TRAVbach | <i>Traversia bacharoides</i> | traversia | Composite |
| TRIpra | <i>Trifolium pratense</i> | red clover | Dicot |
| TRIrep | <i>Trifolium repens</i> | white clover | Dicot |
| ULEeur | <i>Ulex europaeus</i> | gorse | Dicot |
| UNC | <i>Uncinia</i> spp. | hook grasses (a sedge) | Sedge |
| UNCcla | <i>Uncinia clavata</i> | clubbed hook grass | Sedge |
| UNClax | <i>Uncinia laxiflora</i> | | Sedge |
| UNClep | <i>Uncinia leptostachya</i> | | Sedge |

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| UNCrub | <i>Uncinia rubra</i> | red hook grass | Sedge |
| UNCrup | <i>Uncinia rupestris</i> | | Sedge |
| UNCsca | <i>Uncinia scabra</i> | harsh leaved hookgrass | Sedge |
| UNCunc | <i>Uncinia uncinata</i> | matau a Maui | Sedge |
| URTinc | <i>Urtica incisa</i> | scrub nettle | Dicot |
| VERser | <i>Veronica serpyllifolia</i> | turf speedwell | Dicot |
| VERtha | <i>Verbascum thapsus</i> | woolly mullein | Dicot |
| Vicia | <i>Vicia</i> spp. | vetch species | Dicot |
| VIOcun | <i>Viola cunninghamii</i> | native violet | Dicot |
| VIOfil | <i>Viola filicaulis</i> | forest violet | Dicot |
| Vulpia | <i>Vulpia</i> spp. | hair grass | Grass |
| WAHalb | <i>Wahlenbergia albomarginata</i> | harebell | Dicot |
| WAHgra | <i>Wahlenbergia gracilentia</i> s.l. Allan | harebell | Dicot |

7 References

- Allan, H. H. 1961. Flora of New Zealand Volume I. Indigenous Tracheophyta, Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones. P. D. Hasselberg, Government Printer, Wellington, New Zealand.
- Ash, J. E., and J. P. Barkham. 1976. Changes and Variability in the Field Layer of a Coppiced Woodland in Norfolk, England. *Journal of Ecology* **64**:697-712.
- Bannister, P. 1984. Winter frost resistance of leaves of some plants from the Three Kings Islands, grown outdoors in Dunedin, New Zealand. *New Zealand Journal of Botany* **22** 303 - 306
- Bannister, P., and K. L. Wildish. 1982. Light compensation points and specific leaf areas in some New Zealand ferns. *New Zealand journal of botany* **20**:421-424.
- Barker, J., and A. Willmot. 1985. Preliminary studies on the breeding systems of *Dryopteris filix-mas* (L.) Schott and *D. dilatata* (Hoffm) A. Gray. *Proceedings of the Royal Society of Edinburgh* **86**:455-456.
- Bauer, H., C. Gallmetzer, and T. Sato. 1991. Phenology and Photosynthetic Activity in Sterile and Fertile Sporophytes of *Dryopteris filix-mas* (L.) Schott. *Oecologia* **86**:159-162.
- Benedict, R. C. 1936. A Catalog of Hardy Ferns. *American Fern Journal* **26**:74-75.
- Brandes, D. 1995. The flora of old town centres in Europe. Pages 49-58 *in* H. Snkopp, M. Ntimata, and A. Huber, editors. *Urban Ecology as the Basis of Urban Planning*. SPB Academic Publishing bv, Amsterdam, The Netherlands.
- Brownsey, P. J., and J. C. Smith-Dodsworth. 1989. *New Zealand Ferns and Allied Plants*. David Bateman Ltd. 32 - 34 View Rd, Glenfield, Auckland 10, New Zealand.
- Brownsey, P. J., and J. C. Smith-Dodsworth. 2000. *New Zealand Ferns and Allied Plants*. David Bateman Ltd. 32 - 34 View Rd, Glenfield, Auckland 10, New Zealand.
- Burga, C. A. 1999. Vegetation development on the glacier forefield Morteratsch (Switzerland). *Applied Vegetation Science* **2**:17-24.
- Burrows, C. J., and J. K. Watson. 2000. The ecological resotoration of Otamahua/Quail Island 3. Problem plants and their control. *New Zealand Natural Sciences*:11-32.
- Butaye, J., H. Jacquemyn, and M. Hermy. 2001. Differential Colonization Causing Non-Random Forest Plant Community Structure in a Fragmented Agricultural Landscape. *Ecography* **24**:369-380.
- Chater, M. 2002. Waipara River water resource report. Canterbury Regional Council report U **2**.
- Chazdon, R. L. 1988. Sunflecks and their importance to forest understorey plants. *Advances in Ecological Research* **18**:1 - 63.
- Connor, H. E. 1992. The poisonous plants in New Zealand. Department of Scientific and Industrial Research, GP Publications Ltd, New Zealand.
- Coomes, D. A., R. B. Allen, W. A. Bentley, L. E. Burrows, C. D. Canham, L. Fagan, D. M. Forsyth, A. Gaxiola-Alcantar, R. L. Parfitt, W. A. Ruscoe, D. A. Wardle, D. J. Wilson, and E. F. Wright. 2005. The Hare, the Tortoise and the Crocodile: The Ecology of Angiosperm Dominance, Conifer Persistence and Fern Filtering. *Journal of Ecology* **93**:918-935.
- Cooper, A. 1984. Application of multivariate methods to a study of community composition and structure in an escarpment woodland in northeast Ireland. *Plant Ecology* **55**:93-104.

- Cooper, K. M. 1977. Endomycorrhizas affect growth of *Dryopteris filix-mas*. Transactions of the British Mycological Society **69**:161-164.
- Crawley, M. J. 2005. Statistics: An introduction using R. J. Wiley, Chichester, West Sussex, England.
- Dept of Conservation. 2010. Protecting and restoring our natural heritage - A practical guide - Appendix one: Invasive weeds.
- Diez, J. M., J. J. Sullivan, P. E. Hulme, G. Edwards, and R. P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters **11**:674-681.
- Dixon, J. M. 1991. *Avenula* (Dumort.) Dumort. Journal of Ecology **79**:829-865.
- Drake, J. A. 1991. Community assembly mechanics and the structure of an experimental species ensemble. The American Naturalist **137**:1 - 26.
- During, C. 1984. *Fertilisers and Soils in New Zealand Farming*. Ruakura Agricultural Research Centre, Ministry of Agriculture and Fisheries. Government Printer, Wellington, New Zealand.
- Ebbett, R. L., and J. Ogden. 1998. Comparative seedling growth of five endemic New Zealand podocarp species under different light regimes. New Zealand journal of botany **36**:189-201.
- Ecroyd, C. E., and E. G. Brockerhoff. 2005. Floristic changes over 30 years in a Canterbury Plains kanuka forest remnant, and comparison with adjacent vegetation types. New Zealand Journal of Ecology **29**:279.
- eFloras. 2010. Flora of North America: Volume 2 Pteridophytes and Gymnosperms August 2010, http://www.efloras.org/flora_page.aspx?flora_id=1.
- Ellenberg, H., and C. Leuschner. 2010. Vegetation Mitteleuropas mit den Alpen. Zusatzmaterialien zum UTB-Band, Stuttgart.
- Falkengren-Grerup, U. 1986. Soil acidification and vegetation changes in deciduous forest in southern Sweden. Oecologia **70**:339-347.
- Falkengren-Grerup, U., J. Brunet, M. E. Quist, and G. Tyler. 1995. Is the Ca:Al ratio superior to pH, Ca or Al concentrations of soils in accounting for the distribution of plants in deciduous forest? Plant and Soil **177**:21-31.
- Fraser-Jenkins, C. R. 1986. A classification of the genus *Dryopteris* (Pteridophyta: Dryopteridaceae). Bulletin of the British Museum of Natural History (Botany) **14**:183 - 218.
- Godefroid, S., and N. Koedam. 2004. Interspecific variation in soil compaction sensitivity among forest floor species. Biological Conservation **119**:207-217.
- Harley, J. L., and E. L. Harley. 1987. A Check-List of Mycorrhiza in the British Flora-Addenda, Errata and Index. New Phytologist **107**:741-749.
- Henshaw, A. 2012. *Factors influencing future canopy composition at Tiromoana Bush, North Canterbury*. Thesis, University of Canterbury.
- Hepden, P. M. 1960. Studies in vesicular-arbuscular endophytes. II Endophytes in the Pteridophyta, with special reference to Leptosporangiate ferns. Transactions of the British Mycological Society **43**.
- Hill, M. O., J. Mountford, D. Roy, and R. Bunce. 1999. Ellenberg's indicator values for British plants. ECOFACT Volume 2 Technical Annex. Institute of Terrestrial Ecology.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **9**:761-770.
- Hoshizaki, B. J., and K. A. Wilson. 1999. The Cultivated Species of the Fern Genus *Dryopteris* in the United States. American Fern Journal **89**:1-98.

- Howell, C. 2008. Consolidated list of environmental weeds in New Zealand. Science & Technical Publishing, Department of Conservation PO Box 10420, Wellington 6143, New Zealand.
- Hurst, J. M., and R. B. Allen. 2007. The Recce Method for Describing New Zealand Vegetation - Expanded Manual. Landcare Research, Lincoln, New Zealand.
- Ivanova, D., and H. Piekos-Mirkowa. 2003. Chromosome numbers of Polish ferns. *ACTA BIOLOGICA CRACOVIENSIA Series Botanica* **45**:93-99.
- Jiménez, A., and L. Quintanilla. 2009. Biología reproductiva y genética de poblaciones de *Dryopteris corleyi* y sus especies parentales, un complejo diploide-poliplóide. *Capetulo* **4**:81.
- Johnson, P. 2004. Otago Peninsula Plants. An annotated list of vascular plants growing in wild places. Save the Otago Peninsula, Dunedin.
- Jongman, R. H. G., Ter Braak, C.J.F., Van Tongeren, O.F.R., editor. 1995. Data Analysis in Community and Landscape Ecology. Press Syndicate of the University of Cambridge, The Pitt Building, Trumpington St, Cambridge.
- Kawai, H., T. Kanegae, S. Christensen, T. Kiyosue, Y. Sato, T. Imaizumi, A. Kadota, and M. Wada. 2003. Responses of ferns to red light are mediated by an unconventional photoreceptor. *Nature* **421**:287-290.
- Kelly, D., and J. P. Skipworth. 1984. *Tradescantia fluminensis* in a Manawatu (New Zealand) forest: I. Growth and effects on regeneration. *New Zealand journal of botany* **22**:393-397.
- Kimball, S., and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* **17**:1681 - 1693.
- Korpelainen, H. 1994. Growth, sex determination and reproduction of *Dryopteris filix-mas* (L.) Schott gametophytes under varying nutritional conditions. *Botanical Journal of the Linnean Society* **114**:357-366.
- Korpelainen, H. 1995. Growth and reproductive characteristics in artificially formed clonal gametophytes of *Dryopteris filix-mas* (Dryopteridaceae). *Plant Systematics and Evolution* **196**:195-206.
- Korpelainen, H. 1996. Intragametophytic selfing does not reduce reproduction in *Dryopteris filix-mas*. *Sexual Plant Reproduction* **9**:117-122.
- Lambdon, P. W., and P. E. Hulme. 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. *Journal of Biogeography* **33**:1116-1125.
- Landcare_Research. 2010. Poisonous Plants in New Zealand - Scientific Names Index. Landcare Research, New Zealand.
http://www.landcareresearch.co.nz/publications/infosheets/poisonplants/poisonplants_index.asp.
- Leathwick, J. R., F. Morgan, G. Wilson, D. Rutledge, M. McCloud, and K. Johnston. 2002. Land Environments of New Zealand: A Technical Guide. Ministry for the Environment, Wellington, New Zealand.
- Leathwick, J. R., F. Morgan, G. Wilson, D. Rutledge, M. McCloud, and K. Johnston. 2003. Land Environments of New Zealand Nga Taiao o Aotearoa. David Bateman Ltd, Auckland, New Zealand.
- Ledgard, N. 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management* **141**:43-57.

- Legendre, P., and L. Legendre. 1998. Numerical Ecology: Developments in Environmental Modeling. Elsevier, Amsterdam/New York.
- Lemmon, P. E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* **55**:667 - 669.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**:975-989.
- Liao, J.-X., M.-X. Jiang, and H.-D. Huang. 2013. Growth characteristics of *Adiantum reniforme* var. *sinensis* and *A. capillus-veneris* in response to light and soil moisture. *Nordic Journal of Botany* **31**:500-504.
- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2007. Invasion Ecology. Blackwell Publishing.
- Ludlow, C. J., and F. T. Wolf. 1975. Photosynthesis and Respiration Rates of Ferns. *American Fern Journal* **65**:43-48.
- Lusk, C. H., R. P. Duncan, and P. J. Bellingham. 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp–broadleaved forest. *New Zealand Journal of Ecology* **33**:83-89.
- Macleod, N. S. M., A. Greig, J. M. Bonn, and K. W. Angus. 1978. Poisoning in cattle associated with *Dryopteris filix-mas* and *D. borreii*. *Veterinary Record (UK)*.
- McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.
- McDonald, D., and D. A. Norton. 1992. Light environments in temperate New Zealand podocarp rain-forests. *New Zealand Journal of Ecology* **16**:15-22.
- Mitchell, G. B., and E. B. Wain. 1983. Suspected male fern poisoning in cattle. *Veterinary Record* **113**:188.
- Morgan, M. D., and D. A. Norton. 1992. Growth response to light of *Carex inopinata* Cook, an endangered New Zealand sedge. *New Zealand journal of botany* **30**:429-433.
- Norton, D. A. 2004. Kate Valley Conservation Management Area (CMA): Tiromoana Bush Restoration Project Management Plan. University of Canterbury, Christchurch, New Zealand.
- Norton, D. A., A. Leighton, and H. Phipps. 2005. Otamahua/Quail Island Restoration Plan. Conservation Research Group, University of Canterbury, Christchurch, N.Z.
- Parks, J. 2008. The War on Pests: Dealing to key pest plant and animals that threaten native species. A landowners guide for Banks Peninsula and Kaitorete Spit. Banks Peninsula Conservation Trust and Environment Canterbury, Christchurch.
- Penuelas, J., J. Sardans, J. Llusià, S. M. Owen, J. Carnicer, T. W. Giambelluca, E. L. Rezende, M. Waite, and Ü. Niinemets. 2010. Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology* **16**:2171-2185.
- Perring, F., and S. M. Walters. 1962. Atlas of the British Flora. Botanical Society of the British Isles. [London]
- Pigott, C. D., and K. Taylor. 1964. The Distribution of Some Woodland Herbs in Relation to the Supply of Nitrogen and Phosphorus in the Soil. *Journal of Animal Ecology* **33**:175-185.
- Price, J. E., and P. J. Morin. 2004. Colonization history determines alternative community states in a food web of intraguild predators. *Ecology* **85**:1017 - 1028.

- Ricotta, C., S. Godefroid, and D. Rocchini. 2010. Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species. *Diversity and Distributions* **16**:655-662.
- Roovers, P., B. Bossuyt, H. Gulinck, and M. Hermy. 2004. Vegetation recovery on closed paths in temperate deciduous forests. *Journal of environmental management* **74**:273-281.
- Saldaña, A., E. Gianoli, and C. H. Lusk. 2005. Ecophysiological Responses to Light Availability in Three *Blechnum* Species (Pteridophyta, Blechnaceae) of Different Ecological Breadth. *Oecologia* **145**:252-257.
- Skre, O., W. C. Oechel, and P. M. Miller. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. *Canadian Journal of Forest Research* **13**:860-868.
- Stewart, G. H., C. D. Meurk, M. E. Ignatieva, H. L. Buckley, A. Magueur, B. S. Case, M. Hudson, and M. Parker. 2009. URBan Biotopes of Aotearoa New Zealand (URBANZ) II: Floristics, biodiversity and conservation values of urban residential and public woodlands, Christchurch. *Urban Forestry & Urban Greening* **8**:149-162.
- Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the Natural Academy of Science, USA* **103** 5841-5845.
- Suominen, J. 1969. The plant cover of Finnish railway embankments and the ecology of their species. *Annals Botanica Fennici* **6**:183 - 235.
- Ter Braak, C. J. F., and P. Smilauer. 2002. Canoco 4.5: Reference Manual and Canodraw for Windows. User's Guide: Software For Canonical Community Ordination (version 4.5). Microcomputer Power.
- UC/JEPS. 2010. *D. filix-mas* (L.) Schott male fern. *in* A. R. Smith and T. Lemieux, editors. Treatment from the Jepson Manual. University of California, Berkeley accessed on 12 August 2010, http://ucjeps.berkeley.edu/cgi-bin/get_JM_treatment.pl?19,27,30.
- USDA. 2010. *Dryopteris filix-mas* (L.) Schott male fern. Plants Profile. United States Dept of Agriculture accessed on 12 August 2010, <http://plants.usda.gov/java/profile?symbol=DRFI2>.
- Vittoz, P., J. Bodin, S. Ungricht, C. A. Burga, and G. R. Walther. 2008. One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *Journal of Vegetation Science* **19**:671-680.
- Von Holle, B., H. R. Delcourt, and D. Simberloff. 2003. The Importance of Biological Inertia in Plant Community Resistance to Invasion. *Journal of Vegetation Science* **14**:425-432.
- Wagner, W. H., Jr. 1951. Review: Cytotaxonomic Analysis of Evolution in Pteridophyta. *Evolution* **5**:177-181.
- Webb, C. J., W. R. Sykes, and P. J. Garnock-Jones. 1988. *Flora of New Zealand Volume IV: Naturalised Pteridophytes, gymnosperms, dicotyledons*. Botany Division, D.S.I.R., Christchurch, New Zealand.
- Williams, J. A., and C. J. West. 2000. Environmental weeds in Australia and New Zealand: issues and approaches to management. *Austral Ecology* **25**:425-444.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall, 2-6 Boundary Row, London, SE1 8HN.
- Willis, A. J., B. F. Folkes, J. F. Hope-Simpson, and E. W. Yemm. 1959. Branton Burrows: The Dune System and its Vegetation. *Journal of Ecology* **47**:249-288.

Wittig, R. 2002. Ferns in a new role as a frequent constituent of railway flora in Central Europe. *Flora - Morphology, Distribution, Functional Ecology of Plants* **197**:341-350.